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CORRELATED INHERITANCE IN OATS OF REACTION TO SMUTS, CROWN RUST, STEM RUST, AND OTHER CHARACTERS [1]

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INTRODUCTION

Loose and covered smut, and stem and crown rust are among the most destructive diseases of oats (*Avena* spp.). These diseases, caused by the pathogens *Ustilago avenae* (Pers.) Jens., *U. levis* (Kell. and Sw.) Magn., *Puccinia graminis avenae* Erikss. and Henn., and *P. coranata avenae* Corda, respectively, result in heavy annual losses both in yield and quality of grain. Frequently heavy losses are incurred from the rusts, which occur in epidemic form over large areas.

The inheritance of reaction to the smuts and rusts of oats and its relation to other characters have been studied by a number of investigators. Such information is of great value to the plant breeder in developing strains of oats highly resistant to the major diseases and possessing desirable agronomic characters. The present study reports the results of experiments on the mode of inheritance of stem and crown rust and smut reaction in several oat crosses. In the cross Iowa No. 444 × Bond the mode of inheritance of certain kernel characters was investigated as well as the possible relation of these characters to smut and rust reaction.

MATERIALS

The progenies used in these studies consisted of the F_2 and F_3 generations of the crosses Iowa No. 444 (C. I. 2331) × Bond (C. I. 2733), Victoria (C. I. 2401) × Richland (C. I. 787), Carleton (C. I. 2378) × (Victoria-Richland, selection from XS1098), and (Victoria × Richland Sel. No. 5544–3) × State Pride (C. I. 1154), and the F_2 generations of Bond (C. I. 2733) × S. D. 334 (C. I. 2884), Nidar (C. I. 3318) × (Victoria × Richland, Sel. No. 5544–3), Anthony (C. I. 2143) × Victoria (C. I. 2401), and Bond (C. I. 2733) × Hawkeye (C. I. 2464). The F_1 generations of the first three crosses mentioned were obtained from T. R. Stanton, of the United States Department of Agriculture. The remainder of the crosses were made at the Wisconsin Agricultural Experiment Station.

All the parental varieties used belong to the species *Avena sativa* L. with the exception of Bond which belongs to *A. byzantina* C. Koch.

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The basis for the classification of Bond is given by Stanton and Murphy (*27*)[3]. Table 1 shows where the parental varieties were developed, their origin, and more important characters.

TABLE 1.—*Origin and description of parental varieties* [1]

Variety	C. I.[2] No.	Developed or introduced by—	Origin	Superior characters
Iowa No. 444	2331	Iowa Agricultural Experiment Station.	Pure line selection from "Rustless" from Iowa.	High yield, moderate resistance to stem rust.
Bond	2733	U. S. Department of Agriculture; from Australia.	Selection from *Avena sterilis* × Golden Rain.	High resistance to crown rust and smut, stiff straw.
Victoria	2401	U. S. Department of Agriculture; from Uruguay.	Mass population of pure lines selected from native oats of Uruguay.	High resistance to crown rust and smut.
Richland	787	Iowa Agricultural Experiment Station.	Pure line selection from Kherson.	Early maturity, high resistance to stem rust.
Carleton	2378	U. S. Department of Agriculture.	Selection from Sixty-Day (Selection 165–1) × Markton.	Early, high resistance to smut, high yield.
Victoria × Richland		do	Selection from Victoria × Richland (XS1098).	High resistance to stem rust and smut.
Do	(Sel. No. 5544–3)	do	do	High resistance to stem rust, crown rust, and smut.
State Pride	1154	Wisconsin Agricultural Experiment Station.	Pure line selection from Kherson.	High yield, thin hull, early maturity.
S. D. 334	2884	South Dakota Agricultural Experiment Station.	Selection from (Markton × Richland) × (Swedish Select × Kilby Hulless).	High resistance to stem rust and smut.
Nidar	3318	University of Alberta; from Agricultural College at Aas, Norway.		Early maturity.
Anthony	2143	Minnesota Agricultural Experiment Station.	Selection from White Tartar (White Russian × Victory).	High yield, high resistance to stem rust.
Hawkeye	2464	Iowa Agricultural Experiment Station.	Selection from Richland × Green Russian.	High resistance to stem rust.

[1] Most of the data in this table were taken from the 1936 Yearbook of Agriculture (*26*).
[2] C. I. = Accession number of the Division of Cereal Crops and Diseases.

EXPERIMENTAL METHODS

FIELD STUDIES

The F_2 and F_3 generations of Iowa No. 444 × Bond, Victoria × Richland, and Carleton × (Victoria × Richland) were grown in 1936 and 1937, respectively, at the University Hill farms, Madison. The F_2 generations of the remaining crosses were grown in 1937. The F_2 and F_3 lines were planted in 5-foot rows with approximately 25 seeds per row. Parental varieties and State Pride were sown at intervals of approximately 30 rows. In 1937 State Pride was included to provide a susceptible host for the increase of crown and stem rust. Plants were classified as either resistant or susceptible to stem and crown rust.

GREENHOUSE STUDIES AND SMUT AND RUST REACTION

The smut studies were conducted in the greenhouse during the winters of 1936–37 and 1937–38. A composite inoculum of loose and covered smut, with a predominance of the former, was used for all tests. The hulls were removed from the kernels prior to inoculation. Approximately 25 kernels were sown for each F_3 line tested. The temperature of the greenhouse during the period from planting to emergence was kept at 20° C., but after emergence the temperature was lowered to 15°. The smut reaction was expressed as the percent-

[3] Italic numbers in parentheses refer to Literature Cited, p. 802.

age of smutted plants. Check rows of State Pride were included in all tests.

The inoculum used in the crown and stem rust greenhouse studies, except where mentioned otherwise, was collected from the field and consisted of several physiologic races. The seedlings were grown in flats. The first leaf was inoculated with crown rust and later the second leaf with stem rust, by using the brushing method. The flats containing the inoculated plants were placed in a lighted moisture chamber for 24 hours at a temperature of 20° C., after which they were removed to a greenhouse kept at 18° C. A heavy epidemic of rust was secured in all cases, except where noted. The seedlings were classified according to their rust reaction into the following standard classes: 0, 1, 2, 3, and 4 described by Murphy (*17*) for *Puccinia*

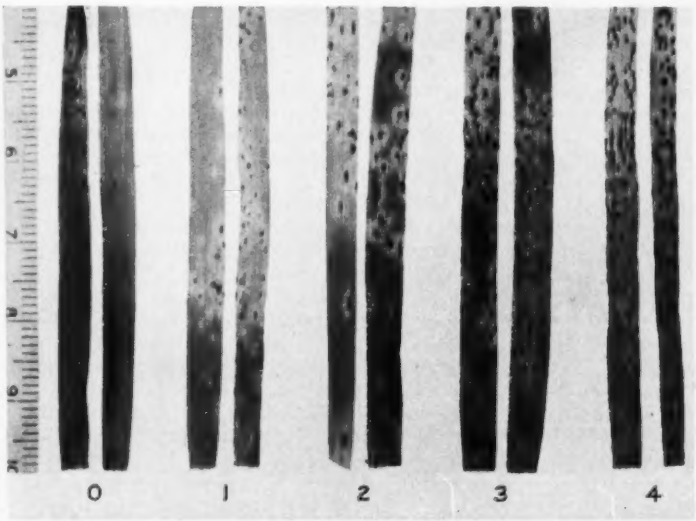

FIGURE 1.—Types of uredinial infection produced by *Puccinia coronata avanae* on seedling plants of oats: Type 0, no infection or necrotic flecks; type 1, small uredia surrounded by necrotic areas; type 2, uredia small to midsized in necrotic or chlorotic areas; type 3, uredia midsized in chlorotic areas, necrosis absent; type 4, large confluent uredia, no chlorosis or necrosis surrounding the uredia. Plants grown at 18° C.

coronata avenae, and by Gordon (*12*) and Levine and Smith (*16*) for *P. graminis avenae*.

The types of uredinial infection produced by *Puccinia coronata avenae* on seedling plants of oats are shown in figure 1. A large majority of the plants fell into classes 0, 1, and 4. For genetic analysis of the data, reaction types 0, 1, and 2 were considered resistant, and 3 and 4 susceptible (*16*). Representative plants of the different reaction classes were transplanted into pots and at heading were inoculated with both crown and stem rust.

During the winter of 1937–38, 67 F_3 lines of Iowa No. 444 × Bond (population 173) were tested in the seedling stage to each of the physiologic races 1, 7, and 46 of *Puccinia coronata avenae*.

EXPERIMENTAL RESULTS

INHERITANCE OF SMUT REACTION

The literature on the inheritance of smut reaction has been reviewed recently by Johnson (*15*) and by Austin and Robertson (*2*). The number of factor pairs involved in resistance to the smuts was found to vary considerably for the different crosses and smut collections used by the different investigators.

The inheritance of smut reaction was studied in the F_2 and F_3 generations of Iowa No. 444 × Bond, and in the F_3 generation of Victoria × Richland and (Victoria × Richland Sel. No. 5544–3) × State Pride. A heavy epidemic of smut was obtained for all crosses save that of Victoria × Richland. The distribution of the F_3 and parental lines for percent of smutted plants, in 10-percent classes, is given in table 2, while the F_2 segregation is given in table 3.

TABLE 2.—*Distribution of F_3 and parental lines for smut reaction to composite inoculum, of the crosses Iowa No. 444 × Bond, Victoria × Richland, and (Victoria × Richland Sel. No. 5544–3) × State Pride*

Cross or parent	Lines in percent smut class indicated											Total lines	Average percent of smutted plants
	0	5	15	25	35	45	55	65	75	85	95		
	No.	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*Percent*
Iowa No. 444 × Bond (population 173)	9	20	21	32	25	11	15	6	7	4	9	159	35
Bond	1	4	1									6	5
Iowa No. 444										2	4	6	93
State Pride											7	7	99
Iowa No. 444 × Bond (population 183)	15	12	18	13	6	8	1	5	7	2	4	91	30
Bond	5											5	0
Iowa No. 444									1	2	1	4	88
State Pride										1	4	5	94
Victoria × Richland	23	13	8	7	4	3	2	1	1	2	1	65	19
Victoria	4											4	0
Richland						1	2	1				4	52
State Pride								4				4	63
5544-3 × State Pride	28	12	17	19	10	3	5	3	1	4	10	112	28
5544-3	5											5	0
State Pride											5	5	99

TABLE 3.—*F_2 smut reaction to composite inoculum for three populations of Iowa No. 444 × Bond*

Cross	Smut free	Smutted	
	Number	*Number*	*Percent*
Iowa No. 444 × Bond	74	47	39
	71	35	33
	68	53	44
Total	213	135	39

The segregation for smut reaction was very similar for all crosses studied. The data agree closely with those found by Johnson (*15*) in the cross Black Mesdag × Victory. Johnson assumed that there were two factor pairs governing the resistance of Black Mesdag: *R* a dominant factor for high resistance, or immunity; and *P*, a supplementary factor for partial resistance. According to this hypothesis one-fourth of the F_3 lines would be expected to possess the factor pair *RR* and have the resistance of the resistant parent, and one-sixteenth

of the F_3 lines would have the factorial constitution *rrpp* and be as susceptible as the susceptible parent.

Two populations of Iowa No. 444 × Bond were tested in the F_3 for smut reaction during the winter of 1936–37. The almost complete susceptibility of State Pride (99 percent smut) and the high percent of smutted plants obtained for Iowa No. 444 (93 percent) indicates that very few susceptible plants escaped smut in the test of Iowa No. 444 × Bond (population 173). The percentage of smutted plants obtained for population 183, while not so high as that for population 173, was sufficient to give a good differentiation for smut reaction. Since the agreement between the two populations for smut reaction is essentially similar, a detailed discussion will be given only for population 173.

The most susceptible parental row of Bond, tested with population 173, contained 14 percent of smutted plants. It is logical to assume that all the F_3 lines of population 173 in the first two infection classes 0 and 5, and approximately one-half of those in the third class, 15, are as resistant as Bond. On this assumption approximately 40, or one-fourth of the F_3 lines, possess the resistance of Bond. Similarly, all the F_3 lines in the 95-percent infection class and most of those in the 85-percent infection class are considered as susceptible as Iowa No. 444. These make up 11 to 13 lines or approximately one-sixteenth of the total population. The number of F_3 lines obtained in the resistant and susceptible classes agree closely with that expected on the basis of two-factor pairs. On the basis of the F_3 segregation, where more than one-factor pair is involved, it is hardly possible to determine the genetic constitution of the F_3 lines with a smut reaction of different degrees of intermediacy between that of the parents.

Three populations of Iowa No. 444 × Bond were tested for smut reaction in the F_2 generation during the winter of 1937–38. The data given in table 3 show that there was an average of 39 percent of smutted plants. No definite conclusions can be drawn from the F_2 data in regard to the number of factor pairs involved in determining smut reaction.

The F_3 generation of Victoria × Richland was tested for smut reaction during the winter of 1936–37. The low percent of smutted plants obtained makes the interpretation of the data difficult. When a level of infection approaching maximum is not obtained, difficulty may be experienced in the genetic interpretation of the data, for plants which escape being smutted are classified as resistant. The average percent of smutted plants for State Pride was only 63, as compared with 94 and 99 obtained with Iowa No. 444 × Bond. It is to be expected that a number of moderately resistant lines would be classified as being as resistant as Victoria on account of susceptible plants that escape infection. If this is taken into account, the 23 lines obtained with the resistance of Victoria agrees fairly closely with the 16 expected, on the hypothesis suggested previously. On the same hypothesis, one-sixteenth, or 4 F_3 lines, would be expected to be as susceptible as Richland. The data in table 2 show that 5 or 6 lines are as susceptible as Richland, and 4 are more susceptible. The transgressive segregation of lines more susceptible than Richland suggests that Richland may have a factor pair for resistance or partial resistance not possessed by Victoria. The evidence for transgressive

segregation, however, is not sufficiently clear to warrant any definite conclusions.

The F_3 generation of (Victoria × Richland Sel. No. 5544–3)× State Pride was tested for smut reaction during the winter of 1937–38. The resistant parent, Sel. No. 5544–3, developed no smutted plants, but State Pride, the susceptible parent, was 99 percent smutted. Assuming that Sel. No. 5544–3 possesses a factor pair for high resistance or immunity epistatic to a second factor pair for partial resistance, one-fourth, or 28 F_3 lines, would be as resistant as Sel. No. 5544–3, and one-sixteenth, or 7 lines, as susceptible as State Pride. This agrees very closely with the 28 resistant and 10 completely susceptible lines actually obtained.

The F_3 distributions for smut reaction of the crosses, Markton × Early Champion and Markton × Ligowa, reported by Coffman et al. (*4*), and of certain of the crosses studied by Reed and Stanton (*22*) are very similar to the distributions found in the present study. Coffman et al. and Reed and Stanton classify all F_3 lines with over 50 percent of smutted plants as succeptible, on which basis their results indicate a single factor. In this study only F_3 lines for which the percent of smutted plants was approximately the same as that for the susceptible parent were classed as susceptible. This separation was based on the assumption that susceptible F_3 lines would not have a higher percentage of escapes than the susceptible parent.

INHERITANCE OF CROWN RUST REACTION

Smith (*24*) recently reviewed the literature on the inheritance of resistance to crown rust. Parker (*20*) concluded that multiple factors controlled crown rust reaction. Davies and Jones (*5*, *6*) and Dietz and Murphy (*8*) report a segregation of 3 resistant to 1 susceptible. Dietz and Murphy (*8*) in the cross Sunrise (resistant) × Fulghum (susceptible), however, obtained an F_2 segregation of 13 susceptible to 3 resistant, which they explain upon the action of 2 factors, one of which is an inhibitor for resistance.

The seedling reaction to a composite collection of crown rust was studied for the F_3 of Iowa No. 444 × Bond (population 183) in the greenhouse during the winter of 1936–37, and for three F_2 populations and several F_3 families in the F_4 of Iowa No. 444 × Bond (population 183) during the winter of 1937–38. The F_3 seedling reaction of Iowa No. 444 × Bond (population 173) to physiologic races 1, 7, and 46 was determined during the winter of 1937–38. Data were obtained on the mature plant reaction of the F_3 of Iowa No. 444 × Bond during the summer of 1937 under a natural epidemic of crown rust.

The segregation for crown rust reaction of Iowa No. 444 × Bond and tests of goodness of fit are given in tables 4 and 5. The segregation found suggests the presence of two factors, *S*, a factor for crown rust resistance, and *I*, a factor which partly inhibits the expression of *S*. On this assumption the genotype of the parents would be Iowa No. 444 (susceptible) *IIss*, and Bond (resistant) *iiSS*. The expression of the inhibitor, when heterozygous, was found to be different for the seedling and mature plant. In the seedling stage the inhibitor was effective in masking the expression of the *S* factor for resistance only when in the homozygous dominant condition. In the mature plant stage under field conditions, however, the inhibitor also was effective, when

heterozygous, in masking the *Ss* genotype but is not potent enough to mask the *ss* genotype.

TABLE 4.—*The inheritance of crown rust reaction for the F_2 of Iowa No. 444 × Bond, in the seedling stage, and tests of goodness of fit*

Values	Segregation of population in indicated infection classes										
	694-1							694-2			
	Resistant				Susceptible			Resistant			
	0	1	2	Total	3	4	Total	0	1	2	Total
Observed	31	12	9	52	15	34	49	21	8	16	45
Expected				56.81			44.39				48.93
χ^2				.93							.75
Range of *P*				0.50–0.30							0.50–0.30

Values	Segregation of population in indicated infection classes									
	694-2			694-3						
	Susceptible			Resistant				Susceptible		
	2	4	Total	0	1	2	Total	3	4	Total
Observed	11	31	42	26	22	23	71	18	34	52
Expected			38.07				69.19			53.81
χ^2							.11			
Range of *P*							0.80–0.70			

The seedling and mature plant reaction expected is shown in table 6. The crown rust reaction of the F_2 and F_3 generations and selected F_4 lines of Iowa No. 444×Bond in tables 4 and 5 in all instances showed good agreement with that expected by the hypothesis suggested. F_1 plants tested in the seedling stage in the greenhouse and in the mature-plant stage in the field had a 1 to 2, and a 3 type of reaction, respectively. Humphrey and Coffman (*13*) report that, under greenhouse conditions, resistance to crown rust was dominant or intermediate in adult F_1 plants from crosses of resistant and susceptible varieties. The segregation of three F_2 populations in the seedling stage (table 4) gave good fits to the 9 resistant to 7 susceptible ratio. In F_3 lines originating from double heterozygous F_2 plants (*IiSs*) the ratio was 9 resistant to 7 susceptible in the seedling stage, and 11 susceptible to 5 resistant in the mature-plant stage. In these lines, both in the greenhouse and in the field, certain plants were more or less intermediate in their rust reaction, which made the classification into resistant and susceptible types somewhat difficult.

In order to provide an additional check upon the segregation of lines grown from *IiSs* plants, the F_4 seedling reaction was determined for seven F_3 families, 183–5 to 183–91, inclusive, which segregated in the ratio of 9 resistant to 7 susceptible in the F_3 seedling tests. The χ_2 values given in table 5 show good fits for each of the seven F_3 families and for the total of all families to the 7: 4: 4: 1 ratio. This

segregation, as expected by the factorial hypothesis suggested, is the same as secured for the F_3 seedling test. In this particular test, the rust epidemic was not so heavy as in previous tests, so an occasional escape was found. The escapes, however, were not sufficiently frequent to upset the results.

TABLE 5.—*The inheritance of crown rust reaction for the cross Iowa No. 444 × Bond and tests of goodness of fit*

Population and inoculum	Observed or expected	Seedling [1] showing indicated reaction				χ values	Range of P
		Resistant	Susceptible	3R:1S [2]	9R:7S [2]		
		Number	*Number*				
F_3 173, race 1	Observed	4	31	12	20	2.08	0.70–0.50
F_3 173, race 7	Observed	3	30	16	18	.48	.95–.90
F_3 173, race 46	Observed	5	28	16	18	.35	.95
	Expected	4.19	29.33	16.76	16.76		
F_3 183, composite	Observed	4	40	24	21	.67	.90–.80
	Expected	5.56	38.94	22.25	22.25		
F_4 183–5, composite	Observed	1	8	2	4	1.15	.80–.70
	Expected	.94	6.57	3.75	3.75		
F_4 183–30, composite	Observed	0	4	4	4	1.71	.70–.50
	Expected	.75	5.25	3	3		
F_4 183–32, composite	Observed	1	4	2	9	8.54	.05–.02
	Expected	1	7	4	4		
F_4 183–49, composite	Observed	1	7	2	4	.85	.90–.80
	Expected	.88	6.13	3.5	3.5		
F_4 183–52, composite	Observed	2	3	6	3	4.88	.20–.10
	Expected	.88	6.13	3.5	3.5		
F_4 183–78, composite	Observed	1	5	5	2	1.55	.70–.50
	Expected	.81	5.69	3.25	3.25		
F_4 183–91, composite	Observed	1	6	0	2	3.70	.30–.20
	Expected	.56	3.94	2.25	2.25		
F_4 Total composite	Observed	7	37	21	28	1.76	.70–.60
	Expected	5.81	40.69	23.25	25.25		

Population and inoculum	Observed or expected	Mature plant [3], showing indicated reaction				χ values	Range of P
		Resistant	Susceptible	3R:1S	11R:5S		
		Number	*Number*				
F_3 173, composite	Observed	12	79	37	45	1.25	0.80–0.70
	Expected	10.81	75.67	43.24	43.24		
F_3 183, composite	Observed	7	79	38	45	2.15	.70–.50
	Expected	10.56	73.94	42.23	42.25		

[1] Grown in greenhouse. [2] R=resistant, S=susceptible. [3] Grown in field.

Sixty-seven F_3 lines of Iowa No. 444 × Bond (population 173) were tested in the seedling stage for their reaction to each of physiologic races 1, 7, and 46 of *Puccinia coronata avenae*. The results (table 5) show that the seedling reaction to individual races of crown rust was the same as that obtained when a composite inoculum was used. The agreement between the reaction of the different lines for the three races was close. A few lines, particular in the two segregating classes, were reversed in their reaction. This may be due to the action of modifying factors.

A close relationship was found between the rust reaction of seedling and mature plants. This is in agreement with the results reported by Parker (*20*) and Smith (*24*).

TABLE 6.—*Seedling and mature plant reactions expected in the cross Iowa No. 444 (IIss) × Bond (iiSS)*

Generation genotype	Phenotypic expression in [1]—				Generation genotype	Phenotypic expression in [1]—			
	Seedling		Mature plant			Seedling		Mature plant	
	F_1 or F_2 plant	F_3 line	F_1 or F_2 plant	F_3 line		F_1 or F_2 plant	F_3 line	F_1 or F_2 plant	F_3 line
F_1, *IiSs*	*r*		*s*		F_2—Cont.				
F_2:					4 *IiSs*	*r*	9*r*:7*s*	*s*	11*s*:5*r*
1 *IISS*	*s*	*s*	*s*	*s*	2 *Iiss*	*s*	*s*	*s*	*s*
2 *IISs*	*s*	*s*	*s*	*s*	1 *iiSS*	*r*	*r*	*r*	*r*
1 *IIss*	*s*	*s*	*s*	*s*	2 *iiSs*	*r*	3*r*:1*s*	*r*	3*r*:1*s*
2 *IiSS*	*r*	3*r*:1*s*	*r*	3*r*:1*s*	1 *iiss*	*s*	*s*	*s*	*s*

[1] *r*=resistant; *s*=susceptible.

INHERITANCE OF STEM RUST REACTION

The literature on the inheritance of stem rust reaction in oats has been reviewed by Smith (*24*). Most investigators, whether they have used a complete inoculum or individual races, have found that resistance to stem rust was dominant and inherited on a single-factor basis.

The seedling and mature plant reaction to a composite collection of stem rust was studied for the F_3 of Iowa No. 444 × Bond, Carleton × (Victoria × Richland), and Victoria × Richland in the greenhouse during the winter of 1936–37. A heavy natural epidemic of stem rust occurred in the oat-breeding nursery during the summer of 1937. Data were taken for the F_3 reaction of the above crosses and the F_2 reaction of several other crosses. The segregation for stem rust reaction and tests of goodness of fit for the F_3 data are given in table 7, and for the F_2 data in table 8.

F_1 plants of Iowa No. 444 × Bond both in the seedling stage in the greenhouse and in the mature plant stage in the field were resistant to stem rust. This is in agreement with the results reported by Humphrey and Coffman (*13*).

TABLE 7.—*F_3 segregation for stem-rust reaction to composite inoculum for the crosses Iowa No. 444 × Bond, Carleton × (Victoria × Richland) and Victoria × Richland, and tests of goodness of fit*

Crosses and place grown	Observed or expected	F_3 lines that were—			χ^2 values	Range of *P*
		Resistant	Segregating	Susceptible		
		Number	*Number*	*Number*		
Iowa No. 444 × Bond (173); field	O	47	79	51	2.07	0.50–0.30
	E	44.25	88.50	44.25		
Iowa No. 444 × Bond (183); field	O	47	79	43	.91	.70–.50
	E	42.25	84.50	42.25		
Iowa No. 444 × Bond (183); greenhouse	O	22	37	20	.42	.90–.80
	E	19.75	39.50	19.75		
Carleton × (Victoria × Richland); field	O	29	63	24	1.29	.70–.50
	E	29	58	29		
Carleton × (Victoria × Richland); greenhouse	O	21	48	15	2.57	.30–.20
	E	21	42	21		
Victoria × Richland; field	O	12	44	25	4.78	.10–.05
	E	20.25	40.50	20.25		
Victoria × Richland; greenhouse	O	4	26	12	5.43	.10–.05
	E	10.5	21	10.5		

TABLE 8.—*F_2 segregation for stem-rust reaction of several crosses under conditions of natural infection in the field, and tests of goodness of fit*

Cross	Observed or expected	F_2 plants—		χ^2 values	Range of *P*
		Resistant	Susceptible		
		Number	*Number*		
Bond × C. I. 2884	O	152	52	0.03	0.90–0.80
	E	153	51		
5544-3 × State Pride	O	175	54	.25	.70–.50
	E	171.75	57.25		
Nidar × 5544-3	O	52	22	.88	.50–.30
	E	55.5	18.5		
Anthony × Victoria	O	73	34	2.62	.20–.10
	E	80.25	26.75		
Bond × Hawkeye	O	100	44	2.37	.20–.10
	E	108	36		

The segregation of the F_3 lines for stem-rust reaction gave fair to good fits to the ratio of 1 resistant: 2 segregating: 1 susceptible, for three crosses studied, both in the seedling and mature-plant stage. Both of the *P* values for Victoria × Richland lie between the 0.10 and 0.05 points, which, being on the border line of significance, is indicative that the observed segregation departs somewhat from the theoretical. These low *P* values are largely the result of too few resistant lines. The number of plants in the heterozygous lines segregating 3 resistant:1 susceptible in the field and greenhouse were 554:193, and 421:142, respectively. The *P* values lay between 0.70 and 0.50, and 0.95 and 0.90, respectively. These values suggest that the small number of F_3 resistant lines found is probably due to chance. The F_2 data for the five crosses given in table 8 all show good fits to the ratio of 3 resistant:1 susceptible.

A separation of the composite inoculum by means of a differential host series according to the key given by Stakman et al. (*25*) indicated the presence of physiologic races 2, 5, and 7. Welsh (*28*) and Smith (*24*) both report that reaction to physiologic races 1, 2, 3, 5, and 7 are dependent upon the same factor pair.

Considerable variation was found in both the number and size of the uredinial pustules within resistant and susceptible lines of all crosses in the field. Separation of homozygous and heterozygous resistant plants was not possible, based upon the number and size of rust pustules. This variation in the number and size of the uredinial pustules of both resistant and susceptible lines was due largely to differences in maturity of the lines. This is illustrated in figure 2. Both the late-resistant and the late-susceptible plants had a greater number and larger uredinial pustules than the early plants. This same relation held for the parental varieties, as the plants adjacent to the alley were a few days later in maturing than those located in the center of the rows. The rust lesions on the late-resistant plants, while numerous, were of a restricted type.

The relation between seedling and mature plant reaction was studied in the F_3 of the crosses Iowa No. 444 × Bond, Victoria × Richland, and Carleton × (Victoria × Richland). Representative plants, classified according to their seedling reaction as having 0, 1, 2, 3, or 4 type of pustules were transplanted into pots and shortly after heading were tested for mature plant reaction in the greenhouse. Also, the relation

was studied for F_3 lines between seedling reaction in the greenhouse and mature-plant reaction in the field. In both instances the agree-

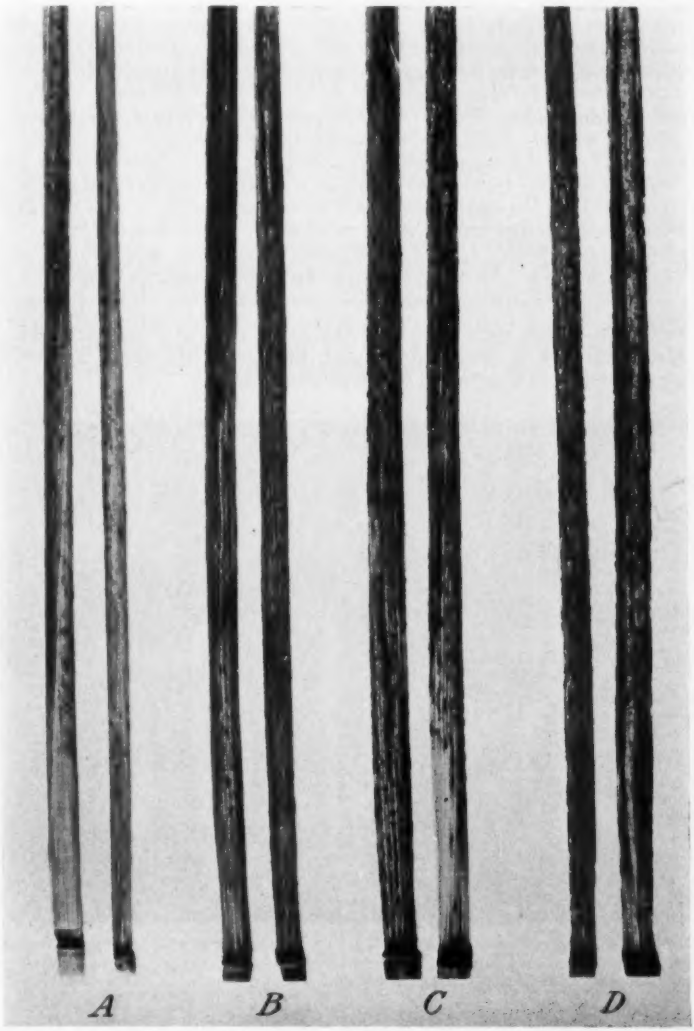

FIGURE 2.—Number and size of uredinial pustules, developing in the field, for F_3 segregates of Iowa No. 444 × Bond: *A*, Early resistant; *B*, late resistant; *C*, early susceptible; *D*, late susceptible.

ment between seedling and mature-plant reaction was very close. This is in agreement with the results of other investigations, reviewed by Levine and Smith (*16*).

INHERITANCE OF KERNEL CHARACTERS FOR THE CROSS IOWA NO. 444 × BOND

The inheritance of 7 kernel characters was studied in the F_1, F_2, and F_3 generations of Iowa No. 444 × Bond. Iowa No. 444 belongs to *Avena sativa* and Bond to *A. byzantiva*. Both species have 21 pairs of chromosomes. A description of the 2 parents for the characters studied, presented in summary form in table 9, is given below.

TABLE 9.—*Comparison of Iowa No. 444 and Bond for several kernel characters*

Variety	C. I. No.	Basal hairs		Basal articulation	Rachilla attachment	Lemma color	Awning	Ratio kernel width to length
		Length	Number					
Iowa No. 444	2331	Short	Few	Solid	Primary	White	Absent	Narrow.
Bond	2733	Medium long.	Many	Sucker	Secondary	Reddish yellow.	Weak awns present.	Wide.

Figure 3, which shows representative kernels of Iowa No. 444, F_1 of Iowa No. 444 × Bond, and Bond, illustrates the main differences in kernel characters between these two varieties.

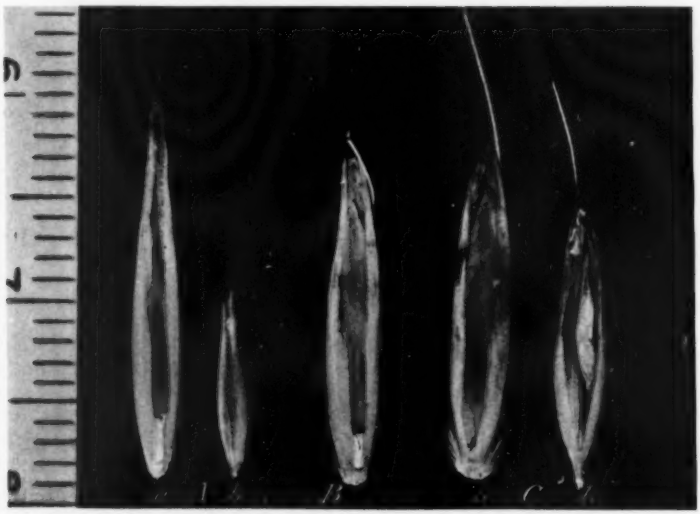

FIGURE 3.—Representative primary (*a*) and secondary (*b*) kernels, of Iowa No. 444 (*A*), primary kernel of F_1 Iowa No. 444 × Bond (*B*), and primary (*a*) and secondary (*b*) kernels of Bond (*C*).

Bond separates from its pedicel by abscission, leaving a small distinct basal scar, commonly called sucker mouth, which is surrounded by a dense tuft of medium long hairs. The second floret separates from the first by basifracture, leaving the rachilla persistent to the second floret. The kernel of Bond is reddish yellow in color, wide in relation to its length, and bears a weak awn.

Iowa No. 444 separates from its pedicel by fracture leaving no scar at the base, commonly called solidified base, which is surrounded by

a few short hairs. The second floret separates from the first by disarticulation leaving the rachilla persistent to the first floret. The kernel of Iowa No. 444 is white, narrow, and awnless.

The F_1 kernels showed a partial dominance of the kernel characters of Iowa No. 444. Table 10 gives the modes of inheritance and tests of goodness of fit for the characters studied based on the segregation of the F_3 lines. A good fit of the observed to the expected ratio is shown for most of the characters. In several instances the *P* values lie between 0.98 and 0.95, as for example the yellow kernel color and awning for population 173, which indicates a closer agreement between the observed and expected ratios than expected by chance. The *P* value for basal hair length of population 173 lies between 0.05 and 0.02. This poor fit is accounted for by too many lines homozygous for short basal hairs and too few for long basal hairs. This same tendency, while not significant, is present in population 183. The number of plants segregating into 3 short and intermediate to 1 long basal hair for the segregating lines of populations 173 and 183 was 890:257, and 954:287, respectively. The *P* values were between 0.05 and 0.02, and 0.20 and 0.10, respectively.

TABLE 10.—*Inheritance of several kernel characters in the F_3 lines of Iowa No. 444 × Bond and tests of goodness of fit*

Class and character	Population 173				Population 183			
	Observed	Expected	χ^2	Range of *P*	Observed	Expected	χ^2	Range of *P*
Basal hair length:	*Number*	*Number*			*Number*	*Number*		
Short	51	45	1.9	0.20–0.10	57	42.8	7.59	0.05–0.02
Segregation	91	90			82	85.6		
Long	38	45			32	42.8		
Type of basal articulation and basal hair number:								
Solid, few	46	45	.12	.95–.90	42	42.8	.04	.98–.95
Segregating	91	90			86	85.6		
Sucker, many	43	45			43	42.8		
Rachilla attachment:								
Primary	41	44.8	.71	.70–.50	46	42.8	.72	.70–.50
Segregating	89	89.6			80	85.6		
Secondary	49	44.8			45	42.8		
Red lemma color:								
Red	42	44.8	.22	.90–.60	37	42.8	2.44	.30–.20
Segregating	91	89.6			83	85.6		
Red absent	46	44.8			51	42.8		
Yellow lemma color:								
Yellow present	42	44.8	.23	.90–.80	42	42.8	.04	.98–.95
Segregating	92	89.6			86	85.6		
Yellow absent	45	44.8			43	42.8		
Awning:								
Awnless and partly awned	47	44.8	.15	.95–.90	43	42.3	.05	.98–.95
Segregating	88	89.6			83	84.6		
Awned	44	44.8			43	42.8		
Partial awning:								
Awnless	12	11.75	.007	.95–.90	18	10	8.53	<.01
Partly awned	35	35.25			22	30		
Ratio of kernel width to length:								
Wide	11	10.5	1.79	.80–.70	12	11.19	1.95	.90–.80
Intermediate	25	21.0			24	22.38		
3 intermediate: 1 wide	38	42.0			42	44.75		
3 intermediate: 1 narrow	45	42.0			50	44.75		
1 wide: 14 intermediate: 1 narrow	38	42.0			43	44.75		
Narrow	11	10.5			8	11.19		

The characters basal hair length and number, basal articulation, and rachilla attachment were monogenic in their inheritance. Fraser (*10*) for the cross Burt × Sixty-Day, and Shaw and Bose (*23*) for crosses between *Avena sativa* and *A. sterilis*, found basal hair length

and basal articulation monogenic. Shaw and Bose (*23*) obtained a dihybrid ratio for basal hair number. Florell (*9*) reports that the type of floret separation in crosses between *A. sativa* and *A. sterilis* is conditioned by a unit factor.

Two-factor pairs were found to govern the inheritance of lemma color, awning, and ratio of kernel width to length. The reddish-yellow color of Bond is the result of the interaction of two-factor pairs, one pair for red, the other for yellow. The color of Bond apparently is similar to that reported for Burt by Fraser (*10*). The segregation of the F_3 lines gave a good fit to the ratio of 1 absent and partly awned; two segregating: one fully awned. Indications, however, were obtained which suggested the presence of a second pair of genes for awning.

The F_3 lines classified as awnless (all plants awnless) and partly awned (some plants awnless and others partly awned) segregated in a ratio of 1 awnless : 3 partly awned, for population 173. The segregation obtained for population 183, however, is a poor fit to the 3 : 1 ratio. The number of partly awned plants in the F_3 lines classified as partly awned varied in number from 1 to practically all of the plants in the lines. Also, the number of spikelets bearing awns on the primary kernels varied from 1 or 2 to practically all of the spikelets. These observations indicate that the expression of this second factor pair for awning is readily influenced by the environment or by other genetic factors. Eight of the approximately 1,500 F_3 plants examined in the fully awned F_3 lines were found to be fatuoids.

The segregation for the ratio of kernel width to length indicates the presence of two-factor pairs. Approximately one-sixteenth of the F_3 lines were homozygous for the wide-kernel type of Bond and one-sixteenth were homozygous for the narrow-kernel type of Iowa No. 444. F_3 lines homozygous for kernel width intermediate between that of the two parents composed approximately one-quarter of the total population.

TABLE 11.—*Linkage intensities between the genes for several kernel characters in two populations of Iowa No. 444 × Bond*

Population and character [1]	Linkage intensity of character indicated				
	Yellow lemma color	Basal articulation and basal hair number	Awning	Rachilla attachment	Hair length
Population 173:					
Basal articulation and basal hair number	39.1±3.8				
Awning	39.9±3.8	0.7±0.4			
Rachilla attachment	40.0±3.8	17.3±2.3	17.3±2.3		
Hair length	53.4±5.2	50.0±5.0	46.0±4.8	33.9±3.5	
Red lemma color	53.4±5.2	51.5±5.1	46.9±4.8	31.8±3.4	30.±0.8
Population 183:					
Basal articulation and basal hair number	29.5±3.5				
Awning	20.5±3.5	3.1± .9			
Rachilla attachment	43.6±4.8	26.6±3.1	27.8±3.2		
Hair length	51.2±5.2	50.0±5.1	49.1±5.1	33.8±3.7	
Red lemma color	52.1±5.2	54.2±5.3	50.0±5.1	39.7±4.0	9.9±1.8

[1] Linear order of genes: Population 173: Yellow lemma color, 39.1; basal articulation and basal hair number, 0.7; awning, 17.3; rachilla attachment, 31.8; red lemma color, 3.0; hair length. Population 183: Yellow lemma color, 29.5; awning, 3.1; basal articulation and basal hair number, 26.6; rachilla attachment, 33.8; hair length, 9.9; red lemma color.

Table 11 shows the linkage intensities between the kernel characters which were calculated from the F_3 data by the method of maximum likelihood described by Immer (*14*). The linear order and distance between the genes as determined from two populations of Iowa No. 444 × Bond are given in footnote 1, table 11. In figure 4 are shown kernels from F_3 plants of Iowa No. 444 × Bond depicting cross-overs between several kernels characters. The linkage between the characters basal articulation and basal hair number was complete, indicating that the same gene pair or two closely linked pairs of genes governed the expression of these two characters. The linear order of the genes as determined for the two populations differed in two respects. The genes for awning, as determined from population 173,

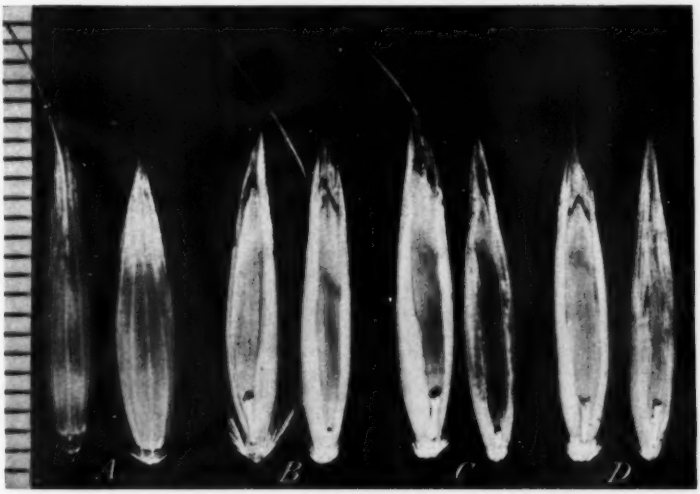

FIGURE 4.—Kernels from F_3 plants of Iowa No. 444 × Bond showing cross-overs between kernel characters: *A*, Awning and basal articulation; *B*, basal hair length and rachilla attachment; *C*, rachilla attachment and basal articulation; *D*, basal hair length and basal articulation.

lay between those for basal articulation and rachilla attachment, whereas for population 183 the order of the genes for basal articulation and awning was reversed. The positions determined for the genes governing red lemma color and basal hair length were reversed in the two different populations. Further study would be necessary to determine the exact linear order of these genes.

The segregation of F_3 lines for width of kernel in relation to the other characters indicated that one of the factor pairs governing this character is closely linked with the factor for rachilla attachment.

Frazer (*10*) from a study of the cross Burt × Sixty Day found a strong linkage between the factors for awning, Burt type of basal articulation, and medium basal hairs. Shaw and Bose (*23*), with interspecific crosses between *Avena sativa* and *A. sterilis* var. *Culta*, obtained crossing-over percentages of 17, 23, and 3.3 between the genes for weak awn and degree of basal pubescence. They, however, obtained no evidence of linkage between basal hair length and num-

ber. Smith (*24*) in the cross Gopher × Rainbow found a linkage between lemma color, awning, and basal hairs.

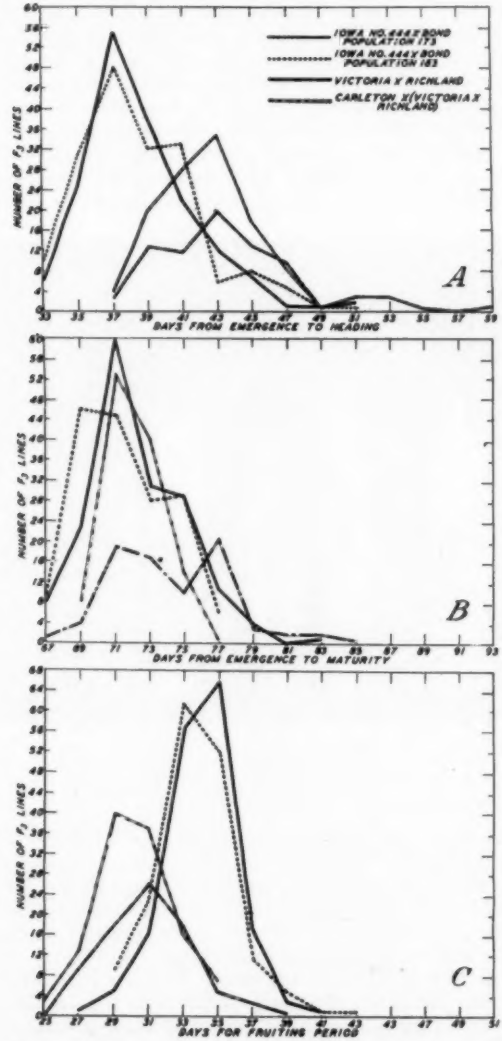

FIGURE 5.—Distribution of days from emergence to heading (*A*), to maturity (*B*), and for fruiting period (*C*) of F_3 lines for the crosses Iowa No. 444 × Bond, Victoria × Richland, and Carleton × (Victoria × Richland).

Nishiyama (*18*) from the study of a series of interspecific crosses, concludes that the *sativa* complex is partially dominant to both the *fatua* and *sterilis* complexes and the *sterilis* complex in turn partially

dominant to the *fatua* complex. Florell (*9*) reports that the complex of characters, oval pitted callus at the base of the spikelet, hairy ring around the callus, hairy rachilla, and strongly geniculate awns on the two lower florets is closely linked in *Avena sterilis* with the factor for the *sterilis* rachilla. Studies of the cross *A. sativa* × *A. fatua* which have been reviewed by Philp (*21*), and Aamodt, Johnson, and Manson (*1*), indicate a complete linkage between the characters of the fatuoid complex, basal articulation, pubescence of base and rachilla, awning, and base type of upper grain. The linkage relationships found in the cross Iowa No. 444 × Bond indicate that other kernel characters, besides those corresponding to the fatuoid complex, are located on the same chromosome.

INHERITANCE OF EARLINESS

The dates when the first, approximately 50 percent, and the last plant headed and matured were recorded for each F_3 and parental line of the crosses Iowa No. 444 × Bond, Victoria × Richland and Carleton × (Victoria × Richland selection from XS1098) in 1937. These data were used in calculating the number of days from emergence to heading and to maturity and length of fruiting period for each line. The fruiting period was taken as the number of days between heading and maturity. The distributions of these data are shown in figure 5, while in table 12 are given the means and standard deviations. The simple correlation coefficients between the three characters are given in table 13.

TABLE 12.—*Means and standard deviations for days from emergence to heading and to maturity, and for fruiting period of F_3 and parental lines for the crosses Iowa No. 444 × Bond, Victoria × Richland, and Carleton × (Victoria × Richland)*

Cross or parent	Number	Emergence to heading		Emergence to maturity		Fruiting period	
		Mean [1]	Standard deviation	Mean [1]	Standard deviation	Mean [1]	Standard deviation
		Days	*Days*	*Days*	*Days*	*Days*	*Days*
F_3 Iowa No. 444 × Bond (173)	167	38.2±0.23	2.91	71.8±0.21	2.72	33.6±0.15	2.00
Iowa No. 444	8	44.0± .18	.53	72.6± .27	.75	28.8± .25	.71
Bond	8	37.8± .16	.45	73.9± .23	.64	36.1± .30	.84
F_3 Iowa No. 444 × Bond (183)	163	37.9± .27	3.42	71.0± .20	2.55	33.2± .17	2.18
Iowa No. 444	10	44.2± .25	.79	73.2± .25	.79	28.9± .31	.99
Bond	10	37.2± .13	.41	73.8± .25	.79	36.6± .30	.96
F_3 Victoria × Richland	80	43.2± .36	3.18	73.9± .33	2.91	30.7± .28	2.50
Victoria	10	55.9± .28	.87	84.1± .29	.74	28.2± .25	.79
Richland	10	39.8± .20	.63	70.1± .31	.99	30.3± .46	1.46
F_3 Carleton × (Victoria × Richland)	116	41.9± .23	2.47	71.6± .14	1.46	29.7± .19	2.02
Carleton	10	40.7± .34	1.06	71.3± .39	1.25	30.6± .31	.97
Victoria × Richland	10	43.3± .68	2.16	71.3± .42	1.33	27.9± .48	1.52

[1] Standard error of the mean shown.

The distributions, both for days from emergence to heading and to maturity, are skewed towards that of the earlier parent, which indicates a partial dominance of earliness. Bond headed approximately 6 days earlier than Iowa No. 444 and matured 1 day later, thus requiring about 7 days longer for fruiting period. The distribution of the F_3 lines for heading shows a preponderance of the lines as early as, or earlier than, Bond, but very few lines later than Iowa No. 444.

In regard to maturity, over one-half of the lines were earlier than either parent, and only a few were later. These distributions suggest that both parental varieties possess factors for earliness which are partly dominant over lateness. The distribution for length of fruiting period is massed towards Bond, the parent with the longer fruiting period.

TABLE 13.—*Simple correlation coefficients between days from emergence to heading and to maturity and fruiting period of the crosses shown in table 12*

Variables correlated	Iowa No. 44×Bond		Victoria× Richland	Carleton× (Victoria× Richland)
	Population 173	Population 183		
Heading to maturity	+0.68	+0.72	+0.70	+0.47
Heading to fruiting	−.60	−.47	−.55	−.81
Maturity to fruiting	+.07	+.26	+.17	+.10
1-percent level	±.21	±.21	±.29	±.24
Pairs number	167	163	80	116

In the cross Victoria × Richland approximately one-quarter of the F_3 lines headed and matured as early as Richland, the early parent, and one-sixteenth as late as Victoria. The distribution suggests that Richland differs from Victoria by at least two-factor pairs for earliness. The (Victoria × Richland) parent used in the cross with Carleton is shown to be heterozygous for days from emergence to heading. Consequently, an interpretation of the F_3 data is not feasible.

The partial dominance of earliness is in agreement with the results reported by Noll (*19*), Garber and Quisenberry (*11*), and Shaw and Bose (*23*). It is very difficult to determine the number of factor pairs involved in the inheritance of a character like earliness. The data suggest, however, that possibly multiple factors are involved in the cross Iowa No. 444 × Bond and at least two in the cross Victoria × Richland. The factorial explanation offered by other investigators varied with the crosses studied. Noll (*19*) reports multiple factors, Caporn (*3*) three factors, and Garber and Quisenberry (*11*) two factors, to govern earliness. Shaw and Bose (*23*) and De Villiers (*7*) obtained evidence of one factor in certain crosses and multiple factors in others.

The correlations between heading and maturity were significant in all cases. The significant negative correlations between heading and fruiting show that in general lines which headed earlier had a longer fruiting period than those which headed later. This was particularly striking in the cross Victoria × Richland.

RELATION BETWEEN CHARACTERS

The independence or association of smut, crown and stem rust reaction with each other and with the characters of days from emergence to heading and to maturity, basal articulation, and basal hair length was measured by χ^2 for Iowa No. 444 × Bond. Since all the kernel characters studied were linked, basal articulation and basal hair length, between which the crossing-over was approximately 50 percent, were used in the χ^2 determinations. The results presented in table 14 show, with two exceptions, that the characters compared are inherited independently. These exceptions, for which the *P* value

lies between 0.05 and 0.02, are crown rust reaction in the field and heading for population 173, and heading and basal hair length for population 183. The P values for a comparison of the same characters of populations 183 and 173 lie between 0.80 and 0.70, and 0.20 and 0.10, respectively. Since at least 2 χ^2 values out of the 49 tested should exceed the 0.05 level by chance and since the P values for the corresponding comparisons in the other population indicate independence, the characters in the two cases discussed above are more than likely inherited independently.

TABLE 14.—*χ^2 tests for independence or association of smut, crown and stem rust reaction, and other characters in the cross Iowa 444 × Bond*

Characters	Population 173			Population 183		
	χ^2 values	Degrees of freedom	Range of P	χ^2 values	Degrees of freedom	Range of P
Smut and crown rust reaction [1]	5.54	6	0.50-0.30	5.37	6	0.50-0.30
Smut and stem rust reaction [1]	5.86	8	.70-.50	4.59	8	.90-.80
Smut reaction and heading	6.76	8	.70-.80	12.47	8	.20-.10
Smut and reaction and maturity	15.50	8	.10-.05	5.05	8	.80-.70
Smut reaction and basal articulation	4.50	8	.90-.80	4.24	8	.50-.30
Smut reaction and basal hair length	7.91	6	.30-.20	8.37	8	.50-.30
Crown and stem rust reaction [1]	1.72	6	.95-.90	4.25	6	.70-.50
Crown rust reaction [1] and heading	14.68	6	.05-.02	3.19	6	.80-.70
Crown rust reaction and maturity	7.40	6	.30-.20	12.55	6	.10-.05
Crown rust reaction and basal articulation	1.34	6	.98-.95	3.78	6	.80-.70
Crown rust reaction and basal hair length	7.82	6	.30-.20	7.67	6	.30-.20
Stem rust reaction [1] and heading	2.96	4	.70-.50	5.24	4	.30-.20
Stem rust reaction [1] and maturity	6.65	4	.20-.10	7.28	4	.20-.10
Stem rust reaction [1] and basal articulation	9.10	4	.10-.05	3.67	4	.50-.30
Stem rust reaction [1] and basal hair length	4.85	4	.50-.30	5.68	4	.30-.20
Heading and basal articulation	7.69	4	.20-.10	3.67	4	.50-.30
Heading and basal hair length	6.89	4	.20-.10	11.25	4	.05-.02
Maturity and basal articulation	9.10	4	.10-.05	2.44	4	.70-.50
Maturity and basal hair length	4.85	4	.50-.30	8.40	4	.10-.05
Crown and stem rust reaction [2]				9.95	6	.20-.10
Crown rust reaction [2] and heading				3.29	6	.80-.70
Crown rust reaction [2] and maturity				3.81	6	.80-.70
Crown rust reaction [2] basal articulation				9.99	6	.20-.10
Crown rust reaction [2] basal hair length				8.35	6	.30-.20
Crown rust [2] and smut reaction				6.57	6	.50-.30
Stem rust reaction [2] and heading				5.08	4	.30-.20
Stem rust reaction [2] and maturity				6.54	4	.20-.10
Stem rust reaction [2] and basal articulation				4.23	4	.50-.30
Stem rust reaction [2] and basal hair length				1.48	4	.90-.80
Stem rust [2] and smut reaction				6.30	4	.20-.10

[1] Mature plant reaction in field.
[2] Seedling reaction in greenhouse.

SUMMARY

A study was made of the mode of inheritance of reaction to a mixed inoculum of loose and covered smuts, *Ustilago avenae* and *U. levis* crown rust, *Puccinia coronata*, and stem rust, *P. graminis avenae*, for several oat crosses. The inheritance of several kernel characters and earliness and their relation to disease reaction was investigated in the cross Iowa No. 444 × Bond.

The F_3 distributions for percent of smutted plants indicate that two factor pairs, one a factor for high resistance, the other a factor for partial resistance, govern the inheritance of smut reaction.

The segregation found for crown rust reaction, in the cross Iowa No. 444 × Bond, suggests the presence of two factor pairs, S a factor for crown rust resistance and I a factor which partly inhibits the expression of S. The masking effect of the inhibitor on the factor S was found to be greater in the mature plant stage in the field than in the seedling stage in the greenhouse. The segregation obtained with

individual races of *Puccinia coronata* was essentially similar to that secured when a composite inoculum was used.

The F_1 seedling reaction indicated a partial dominance of resistance to *Puccinia coronata*, whereas the mature plant reaction in the field showed a partial dominance of susceptibility. In general the agreement between seedling and mature plant reactions was close.

A single factor pair governed the expression of stem rust reaction. Resistance was dominant over susceptibility. A very close agreement was found between seedling and mature plant reaction.

In the cross Iowa No. 444 × Bond, the characters basal hair length and number, basal articulation, and rachilla attachment were monogenic in their inheritance, while the characters, lemma color, awning, and ratio of kernel width to length were digenic. Linkage was found between all the kernel characters studied.

A partial dominance of earliness was found, as judged by days from emergence to heading and to maturity, for the F_3 of Iowa No. 444 × Bond and Victoria × Richland. Significant positive and negative simple correlation coefficients were found between days from emergence to heading correlated, respectively, with days from emergence to maturity, and fruiting period in days.

Smut and crown and stem rust reaction were inherited independent of each other and of the characters' earliness, basal articulation, and basal hair length for the cross Iowa No. 444 × Bond.

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INJURY TO PEA VINES CAUSED BY THE FEEDING OF THE PEA APHID[1]

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INTRODUCTION

The gross effect of aphid feeding on pea plants is easily discernible in the field, but the damage caused to pea vines by the feeding of small numbers of the pea aphid (*Illinoia pisi* Kalt.) has not been fully recognized. It is difficult to distinguish in the field between aphid damage and injury caused by plant diseases and unfavorable climatic or soil conditions. For this reason control measures are seldom used until severe damage has been done.

A more comprehensive knowledge of the injury caused by aphid feeding would be useful in developing a control program and should aid materially in deciding whether or not immediate control measures are necessary at any time in the growth of the plant to prevent injury or complete destruction. To gain more information on the relationships between the growth of the plant, the development of aphid populations, and the extent of injury caused by aphid feeding, a detailed study of the effect of aphid feeding on the pea plant has been made and the data are given in this paper.

MATERIALS AND METHODS

An attempt was first made to carry on this study in the field where a large number of plants were available, but when individual plants were selected for continued observations, weather, fungus, and insect enemies seriously interfered with the work, and satisfactory results were not obtained. Even under greenhouse conditions it was found that keeping records of the aphid infestations and making other daily observations on the plants entailed a time requirement which made it necessary to limit the number of plants to be used, and 60 plants were finally chosen as the unit for the study.

Perfection peas (*Pisum sativum* L.) of the Wisconsin wilt-resistant type were used. The seed was treated with Semesan, Jr., and planted in a mixture of two-thirds compost and one-third sand in 6-inch pots in the greenhouse. Five groups, 12 pots to a group, were planted 1 week apart: the first group was 4 weeks old when the last group was planted. Four seeds were planted in each pot, and about 2 weeks after planting all but one plant in each pot were destroyed; those retained were selected for uniformity in size and vigor.

Young plants did not show extreme differences in size and vigor, but as they grew older such differences appeared, and a number of so-called "strong" and "weak" plants were compared to note the effect of aphid feeding on both types. When the last group of plants was 20 days old from the time of planting, the other groups were respec-

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tively 27, 34, 41, and 48 days old. At this time the height of the plants and the number of internodes were recorded from the growth between the second and the last visible node.

Ten plants were selected to be infested in each group, and two were used as checks. In producing the infestation, one agamic female from a pure line reared on young, uncrowded plants, was placed on the growing tip of each plant before she had started to bear young, and allowed to reproduce for 10 days. All the plants were then covered with 20-mesh screen cages to prevent migration. The tendrils were removed from the plant to prevent their clinging to the cages and disturbing the aphids when the cages were removed. This procedure was followed in order to establish a similar infestation on each plant so that the only variable would be the age and size of the plant. To maintain the plants in suitable condition, they were supported on wooden stakes and watered every 4 days.

No satisfactory method was known for determining the maximum infestation that a plant could withstand and still recover when the aphids were removed. As a rule, as soon as a plant became overcrowded or started to wilt, the older aphids grew restless and began crawling aimlessly about. If the aphids were not removed and counted as soon as this condition developed, an accurate count could not be obtained. If the aphids were removed at this time the plants recovered and could be held for further observation.

This study was carried on between December 24, 1938, and March 27, 1939. The average temperature for the entire period was approximately 60° F. with variations from 55° to 70°, the higher temperatures occurring daily between 10 a. m. and 2 p. m. The relative humidity was approximately 40 percent. With these temperature and humidity conditions, the maximum period that infestations could remain on plants without loss of aphids or plants was determined to be approximately 10 days. This period was arbitrarily set for the removal of all aphids from each plant. At the time the aphids were removed, the height of each plant and the number of internodes were recorded. The plants were retained for continued observations, and additional records were made weekly. A final record of the length of each internode was made at the end of the experiment.

A photographic record of the condition of these plants was made just before the aphids were removed, and a similar record was made of the same plants 18 days later. From these photographs, a series has been selected and presented here to aid in the discussion of the data.

EXPERIMENTAL DATA AND INTERPRETATION

GENERAL EFFECT OF APHID FEEDING

The general effect of aphid feeding was indicated by a wilting of the stipules and leaves at the point of infestation. If the aphid population was sufficiently large and was not removed, individual plants were soon destroyed. If the infestation was removed at the end of 10 days, the plants were stunted only. Weaker plants showed a quicker response in terms of injury than the stronger plants, and younger plants showed the injurious effect of aphid feeding sooner than older plants. The extent of injury appeared to be directly proportional to the number of aphids present and indirectly proportional to the vigor and size of the plant. While the number of plants used for the study

consisted of only 60, with 12 checks, the general effect of feeding was the same for the entire group, with some variations between plants of different age and vigor. As will be shown later, the detailed injury caused by aphid feeding could be noted easily when the aphids were removed and the plants allowed to recover. The stunting of pea plants by aphid feeding was easily duplicated by growing plants in a nutrient solution and substituting water for the solution for a number of days. When the plant was starved except for water, it was only stunted during the period of stravtion. However, that portion of the plant fed on by aphids was not only stunted, but the stipules and leaves became shriveled and dried as a result of the removal of water as well as other plant nutrients.

TABLE 1.—*The effect of aphid feeding on the growth of pea plants 20, 27, 34, 41, and 48 days old, when a single agamic female and her progeny were allowed to remain on the plant for 10 days*

Item	Age of plants	Average number of internodes per plant		Difference between number of internodes of noninfested and infested plants	Average height of plants		Difference between height of noninfested and infested plants	Average progeny produced by 1 adult aphid in 10 days			
		Check	Infested		Check	Infested		Adults	Fourths	Other young	Total
	Days	*No.*	*No.*	*No.*	*Cm.*	*Cm.*	*Cm.*	*No.*	*No.*	*No.*	*No.*
At start of infestation	20	3.0	3.12	------	4.5	5.4	------				
At removal of infestation	30	6.5	6.2	------	13.25	11.5	------	1.1	19.9	55.4	76.4
Increase	------	3.5	3.08		8.75	6.1					
Difference				0.42			2.65				
At start of infestation	27	5.0	5.4	------	11.5	10.9	------				
At removal of infestation	37	9.0	7.9	------	20.25	16.6	------	2.3	21.9	62.1	86.3
Increase	------	4.0	2.5		8.75	5.7					
Difference				1.5			3.05				
At start of infestation	34	7.0	7.5	------	15.5	19.9	------				
At removal of infestation	44	10.5	10.5	------	23.5	25.5	------	3.5	18.8	61.2	83.5
Increase	------	3.5	3.0		8.0	5.6					
Difference				.5			2.4				
At start of infestation	41	10.0	9.7	------	30.5	26.0	------				
At removal of infestation	51	14.0	12.9	------	45.5	37.5	------	11.8	17.6	57.2	86.6
Increase	------	4.0	3.2		15.0	11.5					
Difference				.8			3.5				
At start of infestation	48	11.5	11.3	------	31.5	31.3	------				
At removal of infestation	58	15.0	14.3	------	44.0	40.3	------	7.4	19.2	50.1	76.7
Increase	------	3.5	3.0	------	12.5	9.0	------				
Difference				.5			3.5				

Table 1 shows the average number of aphids present on each group of plants when the infestation was removed. The adults shown for each age group include the original female and those of her young that had reached maturity but had not started to reproduce at the time the aphids were removed. Just why a larger number of the progeny reached the adult stage in the older groups of plants is not known. It may have been due to a better food supply in the larger plants, as the outside environment of all plants was the same. The writers cannot account for the difference in number of adults in the two oldest groups shown.

Some variation occurred in the number of aphids per plant in each age group. There was also a difference in the total average number of aphids per group, but it is thought that these variations caused no significant difference.

The general effect of aphid feeding on pea plants is shown in a series of photographs in figure 1. *A* shows two plants 30 days old; the plant at *a* was infested when 20 days old, the plant at *b* was not infested. *B* shows the same two plants 18 days after the aphids were removed. It will be noted that the number of internodes on the two plants (fig. 1, *B*) is practically the same, but the infested plant at *a* is stunted. Figure 1, *C* and *D*, shows two other plants treated in the same manner; the plant at *C*, *a* was infested when 41 days old. *D* shows the same two plants 18 days after the aphids were removed. The infested plant at *b* blossomed a week later than the noninfested plant at *a*.

DETAILED EFFECT OF APHID FEEDING ON STIPULES, LEAVES, AND INTERNODES

Although stipules and leaves may be destroyed and internodes shortened, a detailed study of aphid feeding showed that if the aphids were removed before the plant was completely destroyed, it could recover and grow to maturity. Aphid feeding stunted or destroyed the stipules and leaves at the point of infestation but did not stop the growth of the plant (fig. 2).

Aphid feeding caused a shortening of the internodes during the time of infestation, but as soon as the aphids were removed the internodes began to lengthen.

The internodes of the younger plants were shortened more than those of the older plants. The diameter of the stem in each case was also reduced by aphid feeding; that is, the part of the stem that grew before or after the infestation was larger than the part that grew during the infestation. The internodes of weak, infested plants were shortened much more than those of stronger plants of the same age (fig. 1, E).

A graphic presentation of the effect of aphid feeding on the internodes of different-aged groups of plants and a comparison between the internodal growth of the infested and noninfested plants are shown in figure 3. In each age group the average length of 10 consecutive internodes for infested and noninfested plants is indicated. In each graph the broken lines represent the average length of internodes from noninfested plants and the solid lines the average length of internodes from infested plants. Internode No. 1 in each graph represents not the length of the first internode of the plants but the length of the second internode below the point of infestation. Line *a* represents the normal growth of 10 consecutive internodes from noninfested plants, and line *b* the corresponding internodes from infested plants. *x*–*x* in line *b* marks the limits of the 10-day infestation.

It was observed that in practically every case the shortening of the internodes began immediately after the plants were infested, showing that the feeding of only a few aphids affected growth. It is also to be noted that as soon as the aphids were removed, the internodes began to lengthen in the plants of all ages, but not to the same extent for each group. In the 20- and 27-day-old groups, the infested plants were slow to recover as was shown by the slow increase in the length of the internodes as compared to those of the noninfested plants. The 20-day-old group was even slower in recovering than the 27-day-old group.

The 34- and 41-day-old groups made good recovery, as expressed by increase in length of internodes. The final internode was even slightly longer in the infested plants than in the noninfested plants.

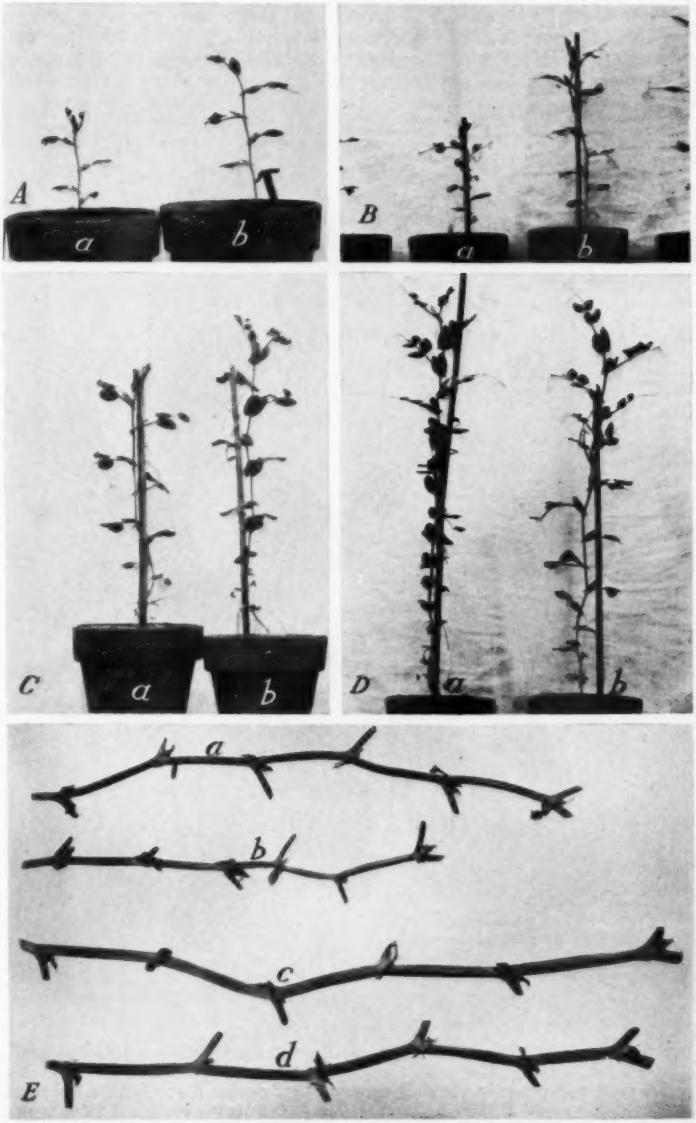

FIGURE 1.—Effect of aphid feeding on pea plants: *A*, Pea plants 30 days old: *a*, Infested when 20 days old with one agamic female aphid; *b*, noninfested. *B*, Same plants as in *A* 18 days after aphids were removed. *C*, Plants 51 days old: *a*, Infested when 41 days old with one agamic female aphid; *b*, noninfested. *D*, Same plants as in *C* 18 days after aphids were removed; infested plant at *b*. *E*, Sections of pea plants of the same age but of different vigor showing internodes shortened by aphid feeding: *a* and *c*, Normal-length internodes; *b* and *d*, internodes shortened by aphid feeding. Aphid feeding injures weak plants *a* and *b* more than strong plants *c* and *d*.

In the 48-day-old group the infested plants showed good recovery for several internodes only and then leveled off. This leveling off in internode length before the length of the noninfested plants was

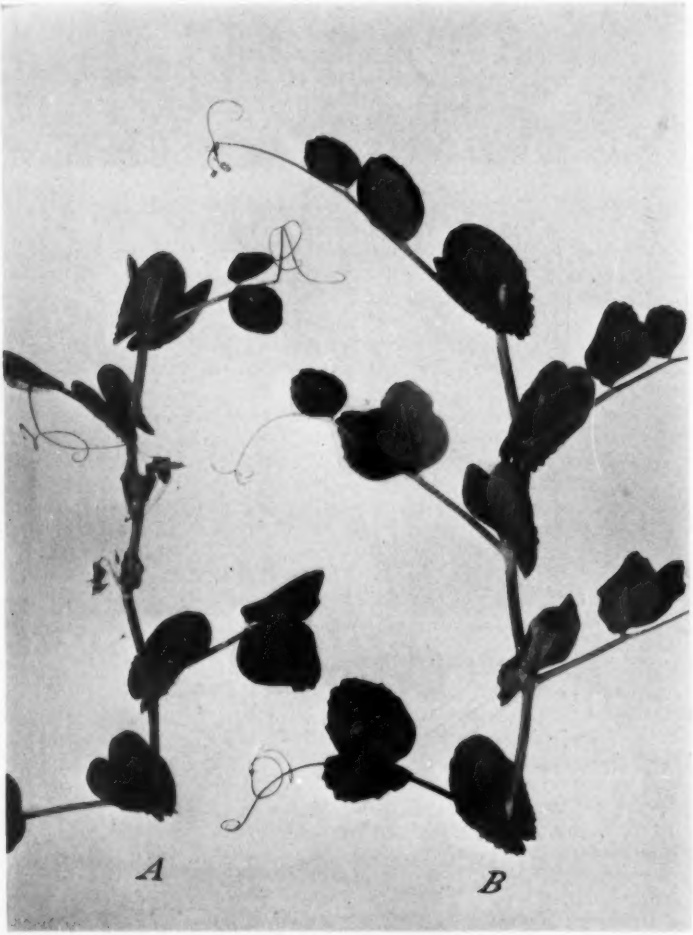

FIGURE 2.—Aphid feeding causes a shortening of internodes and destruction of stipules and leaves during the time of infestation. Stipules and leaves at several subsequent nodes are also reduced in size: *A*, Plant infested with one agamic female when 44 days old and female and progeny removed 10 days after infestation; *B*, noninfested plant of same age as that in *A*.

reached may have been due to the fact that the infested plants bloomed at about this time. As shown in the all-plant average, the infested plants recovered well and finally the length of the internodes equaled that of the noninfested plants.

There was also a tendency toward a slight reduction in the number of internodes produced in an infested plant as compared with that produced in a noninfested plant in the same length of time. The differences for each age group are shown in table 1. It was noted that the leaves and stipules of subsequent nodes were also reduced in

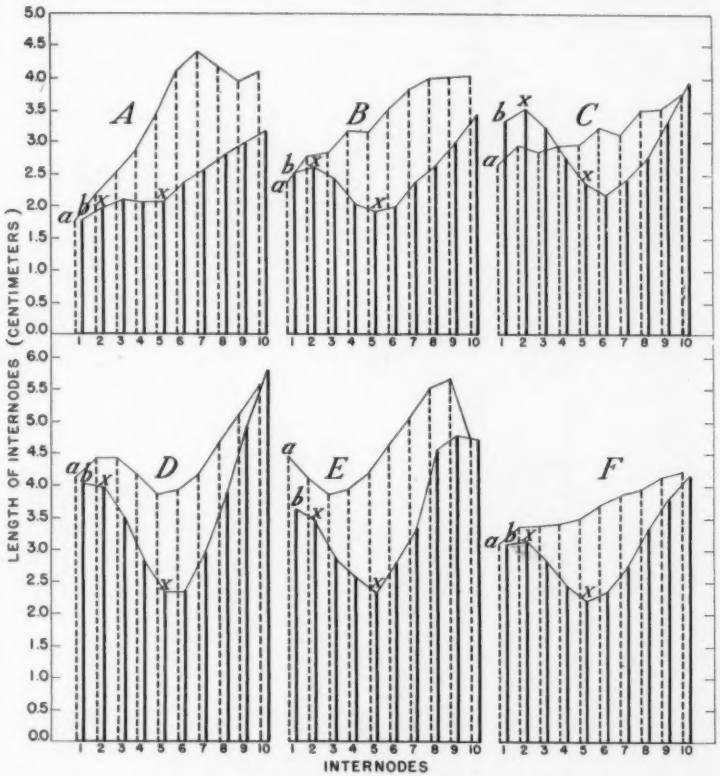

FIGURE 3.—Shortening of the internodes of pea plants of different ages caused by aphid feeding. Plants infested when: *A*, 20 days old: *B*, 27 days old; *C*, 34 days old; *D*, 41 days old; *E*, 48 days old. The all-plant average is shown in *F*. Normal internodal growth of noninfested plants indicated by *a*, of infested plants by *b*, and duration of infestation by *x*–*x*. Figures 1 to 10 at the bottom of each graph represent consecutive internodes. Broken lines represent average length of internodes from noninfested plants and solid lines average length of internodes from infested plants.

size, but reached a more normal size at the later nodes. The stunting of these parts of the pea plant, as indicated before, undoubtedly was due to the removal of plant sap.

The smaller plants were more affected by the aphid feeding than the larger plants. This indicates that an equal population of aphids on a series of plants removed about the same amount of food material, thus demonstrating a difference in the ability of plants of different size and vigor to withstand a loss of plant sap. It is logical to reason that if an

equal amount of water and food were removed from small or weak plants and strong vigorous plants, the injury would be more pronounced on the former. The small plant would also be more stunted and would recover more slowly because of the reduction of leaf surface available for food manufacture.

In table 1 the data show the average number of internodes and height for each age group of plants at the beginning of the infestation and at the time the aphids were removed. The average differences may not appear great for a period of 10 days, but, as shown in figure 1,

FIGURE 4.—Aphid feeding on pea plants near the blossom stage delays blossoming. Two plants of the same age: *A*, Noninfested plant with normal growth and podding; *B*, infested plant on which the first blossom did not appear until 2 weeks after the first blossom on plant shown in *A*.

B and *D*, the injury was very pronounced 18 days after the aphids were removed.

INJURY TO BLOSSOMS AND PODS

In feeding, many species of aphids move from the older and less succulent parts of the plant to the new growth. This is true of the pea aphid, and the greatest population is usually found on the growing tip. When a dozen or more reproducing mothers occur simultaneously on a plant, the increase in population may be such as completely to cover both stem and leaves on the upper portion. As the pea plant develops and the bud cluster opens, aphids settle on the buds, and each blossom pedicle may have a row of aphids feeding along its entire length. Frequently the flower part is also infested inside and out, and quickly withers.

It was interesting to observe how aphid feeding affected the blossoming of plants infested at different stages of growth. When plants 20 and 27 days old were infested at the growing tip with a single reproducing female and the aphids were allowed to remain 10 days, the plant blossomed at about the regular time and at the regular node.

In the plants infested when 34 days old and the aphids removed after 10 days, the blossoms appeared earlier than those on the noninfested plants.

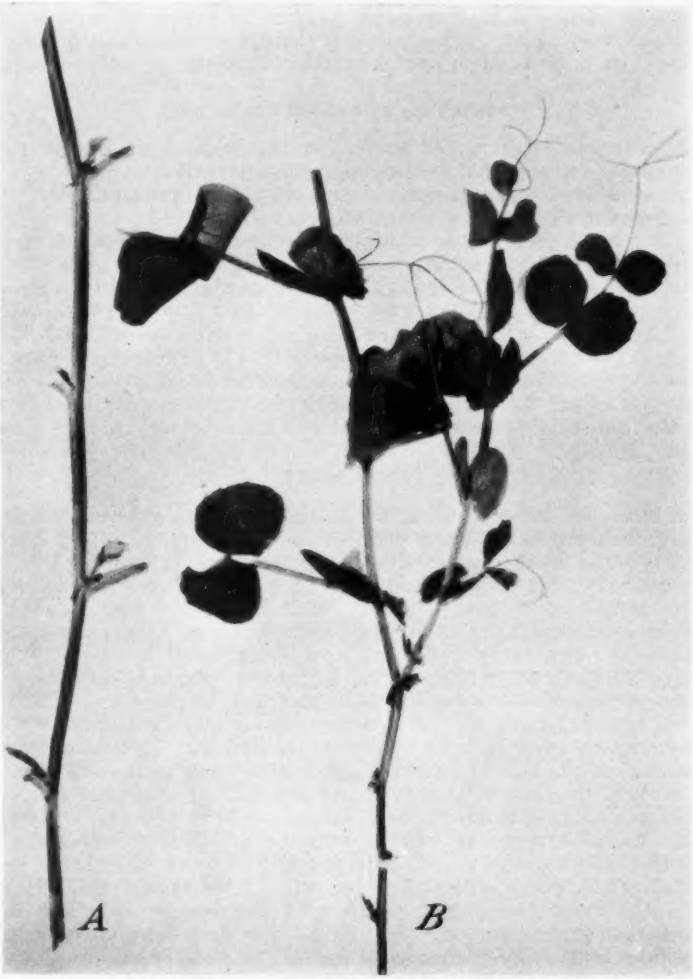

FIGURE 5.—Aphid feeding on pea plants stimulated development of axillary buds below the feeding area several weeks after the aphids were removed: *A*, Injury to growing tip of budding plant stimulated development of flower buds at lower nodes; *B*, similar injury to young plants caused stooling at lower nodes.

Plants infested when 41 days old and the infestation removed after 10 days, blossomed 1 week later than the check plants. Plants infested when 48 days old and treated in the same manner did not blossom until 2 weeks after the check plants (fig. 4).

When plants were infested at the beginning of the blossom stage, no pods were produced during the time of the infestation. Also, it was found that when plants were infested at the top after one or more pods had formed, additional blossoms were blighted and no more pods formed. When the growing tip became overcrowded with aphids, some moved on to the pods and a "crippled" condition developed. The extent of damage was proportional to the number of aphids present.

DEVELOPMENT OF ADVENTITIOUS BUDS

It was found that aphid feeding on the growing tip of pea plants sometimes caused the development of adventitious buds (fig. 5). This condition was not general and probably appeared only when the growing tip was severely injured.

When the tops of young plants were injured, they developed vegetative growth at the axes of the lower leaves (fig. 5, *B*). This condition also develops in the field when plants are injured by frost or other agencies.

Older plants, infested a short time before bloom, produced flower buds at the axes of the upper leaves (fig. 5, *A*). These did not appear until the plant had blossomed at the tip. These adventitious blossoms may have been those that were inhibited at the normal time because of the aphid infestation. These blossoms dropped before or soon after podding.

SUMMARY

A study of the effect of aphid feeding on pea plants was made in the greenhouse to obtain a definite knowledge of the injury caused to pea vines by a controlled aphid population. Plants of five age groups were used for the study and each of these was infested with one nearly mature adult aphid. Each infestation was allowed to remain on the plant for 10 days. Suitable check plants were maintained.

The injurious effect of aphid feeding on pea plants of different ages and vigor is believed to be due to a withdrawal of plant sap. When a single agamic female and her progeny were allowed to remain on any plant for 10 days, definite injury to plants of all ages was demonstrated. If the aphids were not removed as soon as the plant began to wilt, it was soon destroyed. As a result of aphid feeding, the stipules and leaves were reduced in size or destroyed and the internodes were shortened in the area occupied by a limited infestation of aphids. The extent of the injury to pea plants was directly proportional to the number of aphids present. With comparable infestations the injury was more pronounced on younger than on older plants, and on less vigorous than on strongly growing plants. Aphid infestations on older plants caused a delay in the blossoming period of as much as 2 weeks.

Under the controlled conditions of temperature and moisture maintained in these experiments it was found that if a single agamic female was placed on a plant at blossom time and before the pods were set, she and her progeny could cause complete destruction of the blossoms and prevent the development of the pods.

RESISTANCE TO CLUBROOT IN VARIETIES OF TURNIP AND RUTABAGA[1]

By J. C. WALKER

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INTRODUCTION

Clubroot (*Plasmodiophora brassicae* Wor.) continues to be a major disease of crucifers in many countries. Although it has been known for several centuries and has been the subject of numerous scientific investigations during the past 60 years, entirely satisfactory remedial measures have not been worked out for the important crops on which it occurs. Because of the extreme longevity of the pathogen in the soil the disease becomes one of that group in which control is best obtained through the development of disease-resistant varieties. This report concerns one of a series of studies under way on the occurrence and nature of clubroot resistance in the crucifers. The subject has been advanced farthest in the case of the turnip and rutabaga,[2] which are the two crops considered in this paper.

PREVIOUS WORK ON RESISTANCE TO CLUBROOT IN TURNIP AND RUTABAGA

As early as 1853, Anderson (*1*) [3] noted in England that white-fleshed turnips were more subject to clubroot than yellow-fleshed ones. In 1894 Rostrup (*30*) in Denmark stated that rutabagas were more resistant than turnips. No other comments on this subject seem to have been recorded until the present century. In 1902, in a note in the Journal of the Board of Agriculture of Great Britain (*11, p. 149*), it was stated with reference to this disease as follows: "Of late years several so-called disease-proof turnips have been put on the market, and though all are certainly not immune from disease, some are markedly resistant."

The first critical tests of varietal resistance to clubroot in turnip and rutabaga were carried out in 1912 and 1913 in Vermont by Cunningham (*5*). He tested 10 varieties of turnip and the same number of varieties of rutabaga on heavily infested soil in the field. The Southern Curled variety of turnip had 100 percent of infected plants, whereas Early White Milan, Large Amber Globe, Early White Flat Dutch, Strap Leaf, White Egg, Yellow Stone, and Early Snowball each had less than 10 percent of diseased plants. Other varieties tested were between these two extremes. Among the

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[2] The term "turnip" has been used by some to refer to members of both *Brassica rapa* L. and *B. napobrassica* Mill. (*B. campestris* L. var. *napobrassica* DC.). In this paper it is used to refer only to varieties of *B. rapa*. The term "rutabaga" is applied to varieties of *B. napobrassica* which are also commonly referred to in the literature as "swedes" and sometimes erroneously as "yellow turnips."

[3] Italic numbers in parentheses refer to Literature Cited p. 825.

rutabaga varieties there was also a wide range of susceptibility. One variety from India had 95.7 and 95.4 percent of infected plants in 1912 and 1913, respectively. At the other extreme were White Swede, Sweet German, Purple Aberdeen, and Sweet Russian, which showed either no signs of disease or less than 1 percent of the plants infected.

In 1917 Christensen (*4*) in Denmark stated that the English variety Pioneer was highly resistant to clubroot. He also reported the results of a program of improvement in resistance which he had started in 1908 with healthy survivors from two local varieties grown on heavily infested soil. From these, several families were developed that were even more resistant than the variety Pioneer. Two of these families (4 and 25) were tested on infested soil in Wales by Whitehead, who reported them in 1922 (*36*) and again in 1925 (*37*) as distinctly more resistant and productive than other varieties under observation. Family 4 was later introduced by Christensen as Studsgaard Bangholm, while Wilhelmsburger, another resistant variety of rutabaga, was introduced from Denmark about the same time.

In 1924 and 1925 Lindfors (*22, 23*) reported extensive trials of varieties of turnip and rutabaga on clubroot-infested soil in Sweden. Of the fodder turnip varieties he found Svalöf's Yellow Tankard, Dale's Hybrid, Weibull's Sekel, and Weibull's Östersundom the most resistant. Of the rutabaga varieties Studsgaard Bangholm, Wilhelmsburger, Svalöf's Yellow Swedish, and Weibull's Swedish Smooth were the most resistant, while Svalöf's Bangholm, Weibull's Bangholm, Weibull's Imperial, and Weibull's Trondhjem were very susceptible. None of the turnips or rutabagas was completely resistant, however, for even the Studsgaard Bangholm was completely destroyed by the disease on poorly drained, acid soil.

The importance of fodder turnips and rutabagas and the severity of clubroot in the Maritime Provinces, Canada, led to studies of varietal resistance in Nova Scotia by Hockey (*14*) and in New Brunswick by MacLeod (*25; 27, Rpt. 1930*). In Nova Scotia, tests of many varieties showed a high percentage of infected plants in all, but the Herning and Studsgaard strains of Bangholm were usually the least seriously affected by the disease. In New Brunswick, similar results were secured. Selections were made from several strains of Bangholm which were highly resistant. One selection from White Swede, a variety found by Cunningham in Vermont (*5*) to be highly resistant, maintained a high degree of resistance through several generations. A cross between the selection from White Swede and Studsgaard Bangholm gave most promise.

In 1929 Osterwalder (*29*) reported on trials made in Switzerland in 1922 and 1923, in which three varieties of turnip—Gelbe Schmalz, Weisse Schmalz, and Apfel—remained completely free from clubroot in a planting in which cabbage and cauliflower showed high percentages of infection.

In 1931 the Bruce variety of fodder turnip was reported by Findlay (*8*) as capable of producing a commercially successful crop on heavily infested land. This variety had been in use in certain localities in Scotland for upward of 100 years. High percentages of infected plants were found to occur, but the fact that the disease was confined almost entirely to the fibrous roots permitted it to make suc-

cessful growth in spite of the disease. A year later Hendrick (*13*) reported the results of 5 years' trials in Aberdeen County, Scotland, in which Bruce produced satisfactory crops on heavily infested land where other varieties were almost completely destroyed.

Thus, by 1932, the control of clubroot by the use of resistant varieties of turnip and rutabaga had progressed to a marked degree. This was particularly true of the fodder varieties in northern Europe; in New Zealand; and in the Maritime Provinces, Canada, where the culture of these crops comprises extensive acreages. Of the rutabagas, the Wilhelmsburger variety and the Herning and Studsgaard strains of the Bangholm variety continue to be among the most highly resistant (*6, 12, 19, 31, 33, 34*). The Balmoral variety was reported to be successfully resistant in Devon and Cornwall, England, by Beaumont (*3*) in 1933. Of fodder turnips the May variety (Norwegian May, Marienlyst Majturnip) has been found resistant in Denmark (*28*) and in Canada (*27, Prog. Rpt.*). In addition to the reports from Scotland noted above (*8, 13*), Bruce has been shown to be commercially successful as a resistant variety in Canada (*12*), in Devon and Cornwall, England (*3*), and in New Zealand, where a green-topped selection known as Wallace is also satisfactory (*34*). Dale's Hybrid was recorded as highly resistant in Sweden in a report from Svalöf Plant Breeding Institute (*32*) in 1929, confirming the earlier report by Lindfors (*22*); this variety was found to be resistant in Germany also (*24*). The early strain of Bortfelder, Östersundom, reported to be resistant by Lindfors (*22*), was listed as moderately resistant at Svalöf in 1929 (*32*), while the Fünen strain of Bortfelder was reported in 1933 to be resistant in Denmark (*28*). Irvine's Green-Top Yellow turnip was reported to be resistant in New Zealand (*33*), while Yellow Tankard, listed earlier (1924) as resistant in Sweden (*22*), was found to be among the most resistant some 10 years later in eastern Canada (*27, Prog. Rpt.*) and in Finland (*18*). Lorenzen (*24*) listed another variety, Criewener Rübe, as resistant in Germany.

It should be pointed out that the reports of Lindfors (*22, 23*) in Sweden, Hockey (*14*) and MacLeod (*25; 27, Rpt. 1930*) in Canada, and Jamalainen (*18*) in Finland emphasized that under certain conditions so-called resistant varieties showed all or nearly all plants to be infected. Their value lay in the fact that, even in an extremely favorable environment for the pathogen, infection was less damaging to the majority of the plants of resistant varieties, and that under less favorable conditions for infection a much larger proportion of the individuals of the resistant sorts escaped infection. It was also recorded by Findlay (*8*) that in the case of the variety Bruce, which was shown to be eminently productive on heavily infested soil, a large percentage of plants became infected, but the damage was usually negligible because the clubs were confined largely to the secondary roots while the fleshy taproot remained free from disease.

Eriksson (*7*) remarked that round varieties of turnips were less subject to clubroot than long ones. While this may apparently be true it is more likely that the real difference between the two groups is that pointed out by Larson (*20*), who showed that infection of the hypocotyl was relatively rare unless it was wounded. Thus in the round or globe varieties in which the fleshy portion consists chiefly

of enlarged hypocotyl, the incidence of infection and clubbing is quite low as compared with that in the long varieties in which the lower portion of the enlarged storage organ is taproot supporting two zones of fibrous secondary roots through which the fleshy taproot is readily invaded by the clubroot pathogen.

The importance of variation in resistance among species and varieties of the host cannot be finally and satisfactorily evaluated without a knowledge of the variability of the pathogen. The question of physiologic races within the species *Plasmodiophora brassicae* has been raised by a number of investigators. It was suggested by Appel and Werth (*2*) in 1910, by Höstermann (*15*) in 1922, and by Gleisberg (*10*) in 1923, but in no case was definite evidence of this type of specialization presented. In 1931 Gibbs (*9*) reported that he had found no evidence of the existence of physiologic races in New Zealand. In the same year MacLeod (*26*) reported studies in New Brunswick, Canada, wherein inocula collected from a number of cultivated and wild hosts showed no pathogenic differences when used to inoculate a number of varieties of turnip and rutabaga. However, in a later note the same writer (*26, Prog. Rpt.*) reported marked differences in infection of several species and varieties of crucifers when grown on infested soil collected from seven different locations in the Maritime Provinces. Also in 1931 Honig (*16*) reported studies on this subject from Germany. He collected inocula from kohlrabi (*Brassica oleracea* L. var. *caulo-rapa* DC.), cauliflower (*B. oleracea* var. *botrytis* L.), white and savoy cabbage (*B. oleracea* var. *capitata* L.), and from radish (*Raphanus sativus* L.) and studied the degree of infection which resulted when each of these was used to inoculate clubroot-free soil upon which several cruciferous species were grown. The collections from kohlrabi and cauliflower, presumably similar, caused heavy infection on kohlrabi, cauliflower, and *B. nigra* Koch. One of these (kohlrabi collection) was tested on *Camelina sativa* Cr., on which it caused a high percentage of infection. Both inocula caused very low percentages of infection on *Raphanus sativus* and *R. oleiferus*. The collection from savoy cabbage produced heavy infection on *R. oleiferus* but little on *B. nigra*. The inoculum from white cabbage caused a high percentage of infection in *R. oleiferus*, an intermediate percentage on white cabbage and kohlrabi, and a low percentage in *Camelina*. The collection from *R. sativus* infected a low percentage of plants of *Camelina* and of *B. nigra* and a high percentage of plants of *R. oleiferus*. In a later paper Honig (*17*) reported percentages of infection of turnip varieties as follows: Gelbe Schmalz, 7.3; Weisse Schmalz, 27.7; Weisse Wester, 0; Gelbe Wester, 32.6; Apfel Gelbe, 6.2. He pointed out that the first two of these varieties had been reported earlier by Osterwalder (*29*) from Switzerland as completely free from infection on soil where cabbage and cauliflower became heavily clubbed. On the basis of his results, Honig concluded that physiologic races of *P. brassicae* occur. In 1936 Whitehead (*38*) suggested a similar explanation for the fact that in certain of his experimental plots a high percentage of plants of white and savoy cabbage and brussels sprouts became clubbed, whereas varieties of rutabaga which were usually heavily infected in that region were in this case only slightly affected.

SCOPE OF THE PRESENT INVESTIGATION

No critical study of the range of resistance in varieties of turnip and rutabaga used in the United States has been made since the work of Cunningham (*5*) about 25 years ago. The present investigations were started in conjunction with field studies upon the control of clubroot on cabbage by soil treatment, reported upon elsewhere (*21*, *35*). The object of the work was to collect the varieties now in common use in the United States and determine what range in resistance occurs among them.

METHODS AND MATERIALS

The investigation was begun with trials conducted at Franksville, Racine County, Wis., in a portion of the experimental field already described (*21*) in which a high percentage of clubroot occurred on cabbage. The field trials at Franksville were supplemented by similar trials at Madison, Wis., in which soil from the Franksville field was used for inoculum.

Inasmuch as the clubroot organism is very sensitive to changes in soil moisture and reaction, it was found that field trials, though highly indicative, were not entirely reliable, since uncontrollable changes in environment sometimes led to the escape of many susceptible individuals from infection. Greenhouse tests were therefore used extensively as the investigations progressed and eventually were relied upon almost entirely for the final evaluation of a given sample. Muck soil from a heavily infested field a few miles from the Franksville plot was used in the greenhouse studies. For these trials plants were grown upon noninfested soil until the second or third leaf had unfolded, when they were transplanted to infested soil.

In recording disease development at the end of a given experiment, plants were divided into two classes—healthy and diseased—determined by the presence or absence of macroscopic signs of infection. No attempt has been made in the results reported herein to determine grades or degrees of infection within the "diseased" group.

In the course of the greenhouse tests it was found that as the soil was used for repeated trials it tended to become less infectious. At first this was interpreted as a gradual depletion of the pathogen. Examination of the soil showed that, although it was quite acid in reaction (around pH 5.2) when first used, it tended to change toward alkalinity rather rapidly under greenhouse conditions. When it was brought back to pH 5.2 to 5.6 by the addition of dilute sulfuric acid its high infectivity returned.

In view of the fact that physiologic strains of the parasite may exist and thus have a direct influence upon the extent and type of resistance in the host, it was considered desirable to include collections of *Plasmodiophora brassicae* from widely separated localities. Soil or diseased plants from many diseased areas were therefore secured. When only diseased plants were obtained, the macerated clubs were incorporated into acid soil and susceptible plants were grown upon it. Clubs from repeated planting were added to the soil until it became highly infectious. The trials on soils containing the various inocula were all conducted in the greenhouse.

The seeds used in these experiments were all collected from commercial sources.

EXPERIMENTAL RESULTS

TURNIP VARIETIES

The results with turnip in both field and greenhouse are brought together in table 1. The field experiments were carried on in 1932, 1933, and 1934, while the greenhouse tests were made in 1935, 1936, and 1937. The severity of each test may be estimated best by the percentage of infection in the most susceptible variety, Shogoin. Only in the 1934 trial at Franksville was the proportion of diseased plants unusually low for this variety.

Certain varieties remained free from signs of the clubroot disease in all of the trials reported in which they were included. These were May, Snowball, Purple Top Milan, Golden Ball, Rhode Island Rock, Yellow Aberdeen, and Immuna. The last-named variety was developed at and released recently by the Weibull Plant Breeding Institute at Landskrona, Sweden.

TABLE 1.—*Occurrence of clubroot upon varieties of turnip in field trials at Franksville and Madison, Wis., and in greenhouse trials with naturally infested soil from Racine County, Wis.*

Sample No.	Variety	Field trials at—									
		Franksville				Madison					
		1933		1934		1932		1933		1934	
		Plants tested	Plants diseased	Plants tested	Plants diseased	Plants tested	Plants diseased	Plants tested	Plants diseased	Plants tested	Plants diseased
		No.	*Pct.*	*No.*	*Pct.*	*No.*	*Pct.*	*No.*	*Pct.*	*No.*	*Pct.*
22	May	65	0.0	97	0.0	250	0.0	62	0.0	47	0.0
113	Snowball	33	.0	104	.0	256	.0	59	.0	47	.0
142	do	41	.0	16	.0	.....	.....	56	.0	.....	.....
154	Purple Top Milan	45	.0	168	.0	.....	.....	52	.0	25	.0
155	White Milan	40	.0	137	.0	.....	.....	59	.0	40	.0
146	Golden Ball	.....	.....	.....	.....	.....	.....	59	.0	.....	.....
134	Rhode Island Rock	42	.0	.....	.....	.....	.....	54	.0	.....	.....
147	Yellow Aberdeen	24	.0	18	.0	.....	.....	50	.0	.....	.....
200	Immuna	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
143	White Egg	42	.0	40	.0	.....	.....	54	.0	27	.0
152	Seven Top	44	.0	170	1.6	.....	.....	54	.0	66	.0
135	do	47	2.1	56	.0	.....	.....	59	.0	29	.0
151	White Norfolk	44	.0	109	2.8	.....	.....	61	.0	51	.0
139	Pomeranian White Globe	40	2.5	61	.0	.....	.....	51	.0	29	.0
116	Purple Top White Globe	42	2.4	94	.0	235	11.9	51	.0	81	.0
156	do	57	.0	183	.0	.....	.....	54	.0	85	.0
136	do	32	3.1	42	.0	.....	.....	58	6.9	31	.0
137	do	54	3.9	105	.0	.....	.....	57	.0	49	.0
145	Amber Globe	44	9.1	73	.0	.....	.....	54	.0	31	.0
117	Purple Top Strap Leaf	36	11.1	42	2.4	257	12.1	57	14.0	30	.0
138	do	18	5.6	15	6.7	.....	.....	64	.0	.....	.....
144	White Flat Dutch	46	10.9	130	.8	.....	.....	51	.0	67	.0
114	Cowhorn	57	31.6	93	1.1	219	16.0	54	7.4	42	14.3
140	do	45	13.3	64	7.8	.....	.....	61	6.6	77	3.6
141	Bortfelder	47	21.3	39	2.6	.....	.....	52	13.5	29	.0
3991	Earliest White Flat	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
153	Di Rapi	69	88.4	147	1.4	.....	.....	57	71.9	40	.0
115	Shogoin	54	87.0	113	15.9	357	100.0	64	100.0	44	93.2
5808	do	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....

TABLE 1.—*Occurrence of clubroot upon varieties of turnip in field trials at Franksville and Madison, Wis., and in greenhouse trials with naturally infested soil from Racine County, Wis.*—Continued

Sample No.	Variety	Greenhouse trials in Racine County soil									
		1935 No. 1		1936 No. 1		1936 No. 2		1936 No. 3		1937 No. 1	
		Plants tested	Plants diseased	Plants tested	Plants diseased	Plants tested	Plants diseased	Plants tested	Plants diseased	Plants tested	Plants diseased
		No.	*Pct.*	*No.*	*Pct.*	*No.*	*Pct.*	*No.*	*Pct.*	*No.*	*Pct.*
22	May	70	0.0	303	0.0	225	0.0				
113	Snowball	67	.0	178	.0	142	.0	157	0.0	87	0.0
142	do	30	.0								
154	Purple Top Milan	68	.0	120	.0			183	.0		
155	White Milan	66	.0	54	.0			105	.0		
146	Golden Ball							175	.0		
134	Rhode Island Rock			24	.0						
147	Yellow Aberdeen							58	.0		
200	Immuna									96	.0
143	White Egg	68	5.9					178	2.8		
152	Seven Top	66	10.6								
135	do	61	14.8					178	6.7		
151	White Norfolk	58	.0					175	5.1		
139	Pomeranian White Globe	54	9.3	58	8.6			186	7.0		
116	Purple Top White Globe	67	3.0								
156	do	66	6.1								
136	do	57	1.8								
137	do	63	5.0								
145	Amber Globe	68	7.4					167	10.2		
117	Purple Top Strap Leaf	65	30.8					179	23.5		
138	do	44	34.9								
144	White Flat Dutch	68	16.2					174	13.8		
114	Cowhorn	69	40.6					176	25.0		
140	do	56	39.3								
141	Bortfelder	68	36.8	89	29.2						
3991	Earliest White Flat							228	74.1		
153	Di Rapi							123	51.2		
115	Shogoin	66	100.0	96	95.8	132	100.0	153	83.0	76	98.7
5803	do					52	98.1	170	97.6		

In another group of varieties consisting of White Egg, Seven Top, White Norfolk, Pomeranian White Globe, Purple Top White Globe, and Amber Globe, no infected plants occurred in some of the tests; but in other tests a small percentage of the plants, usually less than 10 percent, were diseased.

Purple Top Strap Leaf, White Flat Dutch, Cowhorn, Bortfelder, and Earliest White Flat each showed a considerable percentage of infected plants. The severest test was undoubtedly that conducted in the greenhouse in 1935 (designated as 1935 No. 1 in the table). Except for White Flat Dutch, which had only 16 percent of infected plants, and Earliest White Flat, which was not included in this trial, the percentage of diseased individuals for varieties in this group was 30 percent or higher. In the 1937 No. 1 trial Earliest White Flat had 74 percent infection. These varieties obviously contain a proportion of susceptible plants large enough to sustain considerable losses in clubroot-infested soil.

Di Rapi showed a very high percentage of infection in two trials. It appears to be in the highly susceptible class with Shogoin. Two seed samples of the latter showed 80 percent or more of infected plants in each test in which one or both strains were included except in the 1934 trial at Franksville, where environmental conditions undoubtedly were responsible for the low incidence of disease.

RUTABAGA VARIETIES

The rutabaga trials ran concurrently with those of turnip in both field and greenhouse. The results are presented in table 2. The data from susceptible Shogoin turnip are given in those instances in which it was included. The outstanding feature of the rutabaga trials is the absence of infection in most varieties and the uniformly low percentage of infection in the remaining ones. Under the same conditions Shogoin turnip was heavily infected. It was not surprising to find this low incidence of disease in such varieties as Studsgaard Bangholm and Wilhelmsburger, which have been found to be highly resistant in other regions. What was unexpected was the rarity of clubbed plants in such varieties as Model, Lord Derby, Tipperary, and Magnificent, which are regarded as very susceptible in Wales. In fact, the seed samples of these varieties were secured from T. Whitehead, of Bangor, Wales, who had found them to be among the most susceptible sorts in that region. It is also to be recalled that Hockey (*14*) in Nova Scotia and MacLeod (*25; 27, Rpt. 1930*) in New Brunswick found these and many other varieties of rutabaga to be very susceptible in those areas. These results again raise the question of the occurrence of physiologic races of the pathogen, inasmuch as a generally high resistance of rutabaga varieties has not been reported elsewhere.

TABLE 2.—*Occurrence of clubroot upon varieties of rutabaga in field trials at Franksville and Madison, Wis., and in greenhouse trials with naturally infested soil from Racine County, Wis.*

Sample No.	Variety	Field trials at—									
		Franksville				Madison					
		1933		1934		1932		1933		1934	
		Plants tested	Plants diseased	Plants tested	Plants diseased	Plants tested	Plants diseased	Plants tested	Plants diseased	Plants tested	Plants diseased
		No.	*Pct.*	*No.*	*Pct.*	*No.*	*Pct.*	*No.*	*Pct.*	*No.*	*Pct.*
15	Wilhelmsburger	48	0.0	89	0.0	251	0.0	55	0.0	29	0.0
165	....do			144	.0			159	.0	37	.0
110	White Russian	52	.0	166	.0	263	.0	62	.0	57	.0
111	White Neckless	29	.0	52	.0	278	.0	51	.0	30	.0
148	....do							57	.0		
112	American Purple Top	47	.0					57	.0		
149	....do							52	.0		
150	....do	41	.0					57	.0		
132	Monarch	41	.0	28	.0			60	.0	27	.0
131	Laing's Swede	38	.0	27	.0			61	.0	24	.0
162	Lord Derby			222	.0			157	.0	60	.0
163	Model			115	.0			163	.0	51	.0
164	Tipperary			128	.0			167	.0	47	.0
161	Magnum Bonum			134	.7			154	.0	51	.0
160	Magnificent			259	.4			159	.0	59	.0
16	Studsgaard Bangholm	55	.0	110	1.8	233	.0	59	.0	44	.0
153	Carter's Imperial	53	11.3	61	1.6			54	3.7	24	.0
166											
115	Shogoin Turnip (control)	54	87.0	113	15.9	357	100.0	64	100.0	44	93.2
1											
2											
3											

TABLE 2.—*Occurrence of clubroot upon varieties of rutabaga in field trials at Franksville and Madison, Wis., and in greenhouse trials with naturally infested soil from Racine County, Wis.*—Continued

Sample No.	Variety	Greenhouse trials in Racine County soil											
		1935 No. 1		1935 No. 2		1936 No. 1		1936 No. 2		1936 No. 3		1937 No. 1	
		Plants tested	Plants diseased	Plants tested	Plants diseased	Plants tested	Plants diseased	Plants tested	Plants diseased	Plants tested	Plants diseased	Plants tested	Plants diseased
		No.	*Pct.*	*No.*	*Pct.*	*No.*	*Pct.*	*No.*	*Pct.*[4]	*No.*	*Pct.*	*No.*	*Pct.*
15	Wilhelmsburger	48	0.0			62	0.0	280	0.0	113	.0		
165	....do	52	.0	95	0.0							10	0.0
110	White Russian	52	.0	110	.9							80	.0
111	White Neckless	45	.0			234	1.7	222	.9			30	.0
148	....do	15	.0	17	.0								
112	American Purple Top												
149	....do												
150	....do												
132	Monarch	47	.0	91	.0					61	.0		
131	Laing's Swede	51	.0	28	.0					109	.0		
162	Lord Derby	53	.0	79	1.3							57	.0
163	Model	54	.0	73	4.1							10	.0
164	Tipperary	53	.0	89	.0							37	.0
161	Magnum Bonum	46	.0	106	.9							17	.0
160	Magnificant	51	.0	89	2.4							43	.0
16	Studsgaard Bangholm	51	.0	58	.0	238	.0	245	.0	111	.0		
133	Carter's Imperial	51	2.0	131	2.3					112	.0	19	.0
166										105	.0		
115	Shogoin Turnip (control)									111	92.8		
1												15	.0
2												70	.0
3												53	.0

REACTION OF TURNIP AND RUTABAGA TO INOCULA FROM DIFFERENT REGIONS

The results reported so far were secured from inoculum coming originally from a single county in Wisconsin, and the question of regional variation of the clubroot organism as to its pathogenic selectivity naturally arose. To obtain information on this point inocula were secured in the form of naturally infested soil or as diseased plants from Indiana, Michigan, New York, New Jersey, Massachusetts, and Washington State. When diseased plants were secured the diseased roots were macerated and incorporated into acid muck soil. Several successive crops of susceptible turnip were then grown and in each case the diseased roots were macerated and returned to the soil until it had become highly infectious.

The most susceptible turnip, Shogoin, and Snowball, the one that had remained healthy consistently in the infested Wisconsin soils, were planted in each of the infested soils. The results in table 3 show that Shogoin was readily and quite thoroughly infected by each inoculum. Snowball remained free from infection in all soils except two. Four out of 114 plants were infected in the Indiana soil, while in the soil inoculated from plants received from Washington State 12.2 percent became infected. The American Purple Top rutabaga, which had remained completely free from disease in the Wisconsin field tests, showed no infection in the New York soil, while 10.3 percent of the plants were clubbed in the New Jersey soil.

TABLE 3.—*Occurrence of clubroot on Snowball and Shogoin turnip and American Purple Top rutabaga when grown in the greenhouse upon soil infested with inoculum from various States*

Source of inoculum	Shogoin turnip		Snowball turnip		American Purple Top rutabaga	
	Plants tested	Plants diseased	Plants tested	Plants diseased	Plants tested	Plants diseased
	Number	*Percent*	*Number*	*Percent*	*Number*	*Percent*
Wisconsin	76	98.7	87	0.0		
Indiana	51	98.0	114	3.5		
Michigan	28	100.0	22	.0		
New York	45	100.0	49	.0	20	0.0
New Jersey	21	76.2	23	.0	39	10.3
Massachusetts	24	100.0	30	.0		
Washington	30	93.3	74	12.2		

DISCUSSION

The trials conducted with rutabaga and turnip varieties in Wisconsin soil show a wide range of resistance and susceptibility to *Plasmodiophora brassicae* within the two species of *Brassica*. Insofar as turnip is concerned the results are in general accord with those obtained elsewhere. For instance, the May variety was found resistant in Canada and in Europe, while Amber Globe, White Milan, White Egg, and Snowball were found resistant in Vermont by Cunningham. The chief difference between the results obtained by the writer and those of others lies in the fact that in several varieties no infection whatever was secured in clubroot-infested Wisconsin soils. This is contrary to the results of Cunningham, who usually secured some infection on all varieties, and it differs especially from the results in Canada and in Sweden, where under field conditions high percentages of infected plants often occurred among the so-called resistant varieties. Lindfors (*23*) found that in very acid, poorly drained soil even the resistant forms of rutabaga and turnip were completely destroyed. In the greenhouse trials of this investigation the soil was kept both moist and acid, but this measure did not materially change the results from those in the field nor did it result in any infection whatsoever in the case of several varieties.

The field and greenhouse trials of rutabaga show quite clearly that the inoculum used from Wisconsin soils has little pathogenicity for any of the varieties tested. When this is compared with the incidence of infection on both resistant and susceptible varieties of rutabaga in Canada and in Sweden it must be concluded that either marked differences prevail in the selective pathogenicity of the pathogen in those localities as compared with that in Wisconsin, or some condition of the environment which increases infection in those localities has been overlooked here. While differences in inherent resistance or susceptibility between strains of a given variety are not to be overlooked, it may be pointed out that samples of seed from some of the rutabaga varieties susceptible to clubroot when tested in Wales were found to show little or no infection when grown on clubroot-infested soil in Wisconsin.

In the limited study of inocula from various parts of the United States, including collections from as far east as Massachusetts and as far west as Washington, it appears that they do not differ greatly. It is significant, however, that the Snowball turnip, which remained

healthy throughout many trials with Wisconsin inoculum, was infected in a small percentage of plants when grown on Indiana and Washington inocula and that the American Purple Top rutabaga showed some disease in the New Jersey inoculum. A most exhaustive study of variation of the pathogen within the borders of this country should be carried out. In the meantime it may be assumed that, while cabbage and other members of the kohl group can be expected to be very susceptible to the clubroot organism as it now occurs in the United States, the majority of the varieties of turnip and rutabaga are highly resistant.

SUMMARY

This paper is concerned with a study of the relative resistance and susceptibility to the clubroot organism (*Plasmodiophora brassicae* Wor.) of the varieties of turnip (*Brassica rapa* L.) and rutabaga (*B. napobrassica* Mill.) in common use in the United States.

Insofar as turnips are concerned, the results are in general accord with those secured elsewhere in that certain varieties are highly resistant, others moderately resistant, and still others very susceptible.

Most rutabaga varieties showed no infection when grown on naturally infested Wisconsin soils, and none showed a high percentage of infection. The fact that some of the varieties used are known to be very susceptible to clubroot in certain European localities indicates a possible variation in pathogenic selectivity within the species *Plasmodiophora brassicae*.

A preliminary study of the pathogenicity of the organism collected from several widely separated localities in the United States indicates very little difference in the pathogenic selectivity of the inocula used. However, low percentages of infection were obtained in some cases on varieties of turnip and rutabaga that had remained completely free in tests on naturally infested Wisconsin soil. The importance of further study of pathogenic variability of the parasite is emphasized.

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TOBACCO FOLLOWING BARE AND NATURAL WEED FALLOW AND PURE STANDS OF CERTAIN WEEDS[1]

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INTRODUCTION

In colonial days the growers of tobacco of necessity planted the crop on newly cleared land. It was soon observed that virgin soil produced good yields as well as leaf of high quality well suited to the market demands of the period. Even at that early date the growers of the crop found that after a given field had been used for growing tobacco for a short period the soil became less productive. Consequently the early settlers continually cleared the forested areas in order to consistently produce the desired type of tobacco. It is commonly recognized even today that recently cleared forested land produces a grade of leaf having a fine texture and light body that for many purposes commands a relatively high market price. In recent years, however, the wooded areas have become so limited that it is necessary for growers to produce the major part of the crop on fields that have been cultivated continuously or intermittently for a comparatively long period.

This practice has ultimately resulted in depletion of the available plant-food reserves of the soil so that it has become increasingly necessary to supply soil deficiencies in plant food in the form of manures and fertilizers. It has generally been possible to maintain high yields of tobacco in continuous culture by these practices, provided parasitic diseases do not come in to damage the crop, but it is a common occurrence for the quality of the leaf produced under continuous culture to become unsuited to market demands. In an effort to overcome these difficulties a number of rotation systems in combination with manures and fertilizers have been tried with a fair degree of success. These practices, however, have not proved satisfactory on all soils and with all crop combinations.

The importance of the several plant-food constituents in maintaining yields and values of tobacco has received attention for flue-cured (*10*)[3] and Maryland leaf (*8*). It is always necessary that these constituents be supplied to the plant in available forms either by the soil or as manures and fertilizers applied to the soil.

The possible contributing factors concerned in the effect of a given crop on the succeeding crop in the rotation have been previously discussed in detail in a paper (*5*) that gives a review of the literature bearing upon these relationships.

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[3] Italic numbers in parentheses refer to Literature Cited, p. 844.

It was early recognized (1891) that weed plants occurring as adventitious vegetation along waysides and elsewhere could be used in preparing composts, since they are relatively rich in plant-food constituents (*9*). It was pointed out that the different species varied in composition, as shown by published analyses. Additional data giving analyses of weeds under North Dakota conditions also have been published (*6*). More recently Eisenmenger (*2*, *3*) has conducted studies on the organic decomposition products resulting when plants belonging to various species are incorporated with the soil.

The culture of tobacco in Maryland is unique in that nowhere else in the United States has the crop been grown continuously in a given area for so long a period, about 300 years. This section has furnished the industry with the parent stock for varieties from which many of our important commercial types have developed (*4*). In addition, it has furnished the testing ground for developing practical methods of maintaining yields and quality of tobacco when grown on a given soil for a long period. Killebrew (*7*) in 1880 pointed out that yields could be maintained by the use of manures and fertilizers but that the quality of the product was often unsatisfactory. Further observations in many of the older tobacco-producing States were also presented in regard to the maintenance of yields and quality of tobacco on newly cleared lands and in fields that were allowed to lie idle for a period of years. Patterson (*11*) reported in 1900 that Maryland soils which had lost their capacity to produce high-quality tobacco as a result of continued use in growing this crop could be renovated by allowing them to revert to broomsedge and old-field pine. It has been observed repeatedly, in connection with various experiments conducted over a period of years at the Upper Marlboro tobacco field station, that on cultivating land which had been occupied for a time by native vegetation, consisting of broomsedge or other weeds, tobacco of exceptionally fine quality was obtained for the first and second years following this type of vegetation cover. The crop produced under these conditions more nearly approached that obtained on newly cleared forested areas than under any other set of conditions yet found.

The cause of failure to obtain the type of leaf growth desired in continuous culture is not clear. The exhaustion of plant nutrients undoubtedly is often an important factor, as well as the building up of parasite populations that injure or destroy the growing plant. The development of soil toxins or other substances or conditions deleterious to growth of tobacco appears sometimes to enter the complex, but direct proof or identification of such conditions has not been developed. Apparently the physical condition of the soil induced by, or associated with, the development of adventitious vegetation is a dominant factor in the favorable effects obtained. The mulch produced by the accumulated debris associated with natural weed fallow, by rendering available potassium or other plant foods from the soil minerals (*12*), may be a factor in the favorable effects reported. This mulch also prevents wind and water erosion, which transports considerable topsoil under some conditions.

In an earlier publication (*1*) it was pointed out that it has been possible consistently to produce high-quality leaf under Maryland conditions when the crop follows a natural weed fallow of sufficient duration.

PROCEDURE

Since it had been observed that high-quality tobacco (*Nicotiana tabacum* L.) was consistently produced for the first year or two after a growth of natural weed cover, it seemed desirable to study the subject experimentally. Accordingly, in 1922 experiments were undertaken with tobacco grown after natural weed fallow on plots at the tobacco field station, Upper Marlboro, Md. These plots immediately adjoined those employed in tests with legumes and other cover crops, the results of which have been reported elsewhere (*1*, *5*). The plots as originally designed were one-eighth of an acre in size (36 by 151¼ feet). The tobacco plants were transplanted in rows 36 inches apart and 34 inches apart in the drill. There were two series, in one of which tobacco was grown in a 2-year rotation with weeds. After removal of the tobacco crop in early fall the land was left undisturbed about 20 months until it was plowed for the next tobacco crop in the spring of the second year. In another series the plots were occupied by weeds for an additional year. The period between the successive crops of tobacco in this instance was about 32 months. The soil was undisturbed during these periods, since any disturbance would have altered the natural vegetation cover.

These plots were subdivided crosswise in 1925, one-half of each plot being kept free of weeds by frequent hoeing during the summer months. This procedure was adopted in order to determine whether the bare fallow was as effective in maintaining yields and values as the weed fallow. The tobacco on these plots was fertilized with a 1–7–5 mixture applied at the rate of 1,000 pounds per acre during the period 1925–33 and with a 2–8–12 mixture applied at the rate of 750 pounds per acre beginning with 1934. These mixtures were prepared from nitrate of soda, superphosphate, and high-grade sulfate of potash.

Since tobacco following the natural weed fallow made up of adventitious vegetation consistently gave good yields and values, it was deemed desirable to determine whether any of the several species occurring in the weed complex were more effective than the others. In 1931 tests were inaugurated to determine the effects of some of the more common species on the yields and quality of the tobacco crop when grown in substantially pure stands. The plants growing in the natural weed fallow varied to some extent from season to season, apparently depending upon a variety of conditions, more particularly the weather prevailing during the seed-germination period. There was always a more or less dense cover of vegetation throughout the summer months. In the first year, summer annuals predominated, and there was considerable mixture of legumes and nonlegumes. In the second year, some of these annuals reseeded themselves and in some instances wild grasses, including small broomsedge (*Andropogon virginicus* L.) were observed, but the period was too short for establishment of this old-field weed. The trumpetcreeper (*Tecoma radicans* (L.) Juss.) frequently came in to a considerable extent the second year from old roots remaining in the soil. Frequently in the first year evening-primrose (*Oenothera*) species were prevalent during the spring.

The weed species included in the pure-culture test were annual sweetclover, Hubam strain (*Melilotus alba* Desr.), rabbitfoot clover (*Trifolium arvense* L.), common ragweed (*Ambrosia artemisiifolia* L.),

wild pea (*Strophostyles helvola* (L.) Britton), partridge-pea (*Cassia chamaecrista* L.), horseweed (*Erigeron canadensis* L.), lambsquarters (*Chenopodium album* L.), and annual lespedeza, Kobe strain (*Lespedeza striata* (Thunb.) Hook. and Arn.). Any of these species may occur in the natural weed fallow to a greater or less extent. However, rabbitfoot clover, wild pea, partridge-pea, common ragweed, and horseweed are the species ordinarily found. It was soon observed that seed of rabbitfoot clover and horseweed commonly germinated in the fall. These species, therefore, passed the winter in the seedling stage, whereas wild pea, lambsquarters, partridge-pea, and common ragweed came up in the spring.

The question at once arose as to the procedure necessary to grow these species in pure stands. There was little or no information available in regard to growth habits or requirements of most of the above-mentioned plants. Since they are generally regarded as objectionable, the only information available was concerned with eradication. However, it may be mentioned here that rarely are any of these species troublesome weeds in cultivated crops. In the earlier years of the tests the young plants obtained from old fields were transplanted in rows 1 foot apart, except wild pea, lespedeza, and sweetclover, which were grown from seed. It has been found possible in recent years to grow practically all of these plants from seed. The procedure followed in seeding ragweed, horseweed, and lambsquarters has been to scatter seed heads over the plots on which they are to be grown after the land has been prepared by a light harrowing. The weed crop was generally unfertilized and grew 1 year, followed by tobacco the second year. The tobacco at the Marlboro location was fertilized with a 2–8–12 mixture applied at the rate of 600 pounds per acre. The fertilizer materials used in compounding this mixture were nitrate of soda, dried blood (one-half the nitrogen from each), superphosphate, and high-grade sulfate of potash.

One series consisted of individual plots, not duplicated, of some of these weed species and a control bare-fallow plot. (See table 4.) The plots of this series were one-hundredth of an acre (10½ by 41½ feet), with a 2-foot space between plots. Plantings of tobacco were made in rows 3½ feet apart on each of the treatments. The plants were set 29 inches apart in the row. The tobacco was grown in a 2-year rotation with the species shown. The weed growth on these plots was turned under just prior to or immediately after the first killing frost in the fall.

Another series of tests was carried out, consisting in most instances of duplicate plots (see table 5), with all of the above-mentioned species and, in addition, a bare-fallow and a natural weed-fallow plot. The plots in this series were one-seventieth of an acre (10½ by 59¼ feet). Plantings of tobacco were made in three rows to the treatment, 3½ feet apart, with plants spaced at a distance of 29 inches in the drill. A space of 2 feet was provided between plots to prevent cross feeding. The weed growth in these plots was mashed down in the fall and covered with fine-mesh woven wire to prevent the wind from blowing the material from the small areas involved. As a rule the land was plowed for tobacco in the following April.

The above-described tests at Upper Marlboro were located on Collington sandy-loam soil.

In 1933 additional tests were begun at the Pee Dee Experiment Station, Florence, S. C., on Marlboro sandy loam. The plots in this series were one-fortieth of an acre (16 by 68 feet). The plots were separated by a 2-foot space to prevent washing and cross feeding. The rows for tobacco were spaced 4 feet apart and the plants were set 2 feet apart in the drill. The weeds (see table 6) were transplanted in 8 rows to the plot, 2 feet apart. The season's weed growth was chopped up with a stalk cutter after the first killing frost and turned during January for the tobacco crop the following summer. The tobacco was fertilized with a 3–8–6 fertilizer at the rate of 1,000 pounds per acre. The weed growth received no treatment. The fertilizer mixture used in this series was prepared from nitrate of soda and cottonseed meal, each supplying one-half of the nitrogen; superphosphate; and sulfate and muriate of potash, two units or one-third of the potash being derived from the muriate.

The methods used in culture and handling of the tobacco crops grown in these tests will not be considered in detail, but it should be stated that these methods conformed to the best generally accepted local practices. Every effort was made to give each treatment uniform methods of culture and handling. For example, the transplanting was made across the several plots of each series instead of in the direction of a given treatment, so as to equalize plants as to size, freedom from disease, and vigor. Representative samples were selected from each grade of the several treatments after they were stripped, graded, and weighed. The weights thus obtained were used in making calculations of yields. These samples were later submitted to experienced judges of Maryland tobacco, who assigned values. Calculations of gross values per acre were based on these figures.

It was not a simple matter to grow the several wild species of plants in pure culture, since it was necessary frequently to remove by hand any extraneous species appearing in the cultures. Where the cultures were in rows it was possible to remove the undesired kinds with less expenditure of labor. However, in order that the surface of the soil might be covered thoroughly, broadcast seeding was adopted where possible. It has been evident during the later years that many of the weeds have not grown so well as in the earlier years of the test. This has been particularly evident with the partridge-pea.

EXPERIMENTAL RESULTS

Since the weather has a dominant influence on the survival of transplants and the subsequent growth of the tobacco crop, it cannot be neglected in any attempt to arrive at a better understanding of the growth factors operating under field conditions. The rainfall, as recorded at the location of the experiments at Upper Marlboro, Md., and Florence, S. C., arranged in 10- and 11-day periods, is shown in tables 1 and 2. It is practically impossible to summarize the complete records, since frequently short intervals of 1 or more days occurred when the rainfall or temperature was so abnormal as to determine to a large extent the final growth of the crop. It has happened that 5 to 10 inches of rain in a 24- to 48-hour period resulted in almost complete crop failure. Excessive temperature of a few days' duration at times may produce effects from which the crop never completely recovers. The temperature data are not presented for the Maryland location, but should not be greatly different from

those published for Washington, D. C., about 15 miles distant. The temperature data applicable to the South Carolina location are those published by the United States Weather Bureau for Florence, S. C.

TABLE 1.—*Rainfall at Upper Marlboro, Md., for 10- and 11-day periods during the growing seasons, 1925–37*

Month and date	Rainfall during growing season												
	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	1935	1936	1937
April:	*In.*	*In.*	*In.*	*In.*	*In.*	*In.*	*In.*	*In.*	*In.*	*In.*	*In.*	*In.*	*In.*
1–10	0.20	1.02	1.83	0.00	0.70	2.80	2.11	0.53	1.98	0.22	3.45	2.11	1.14
11–20	.66	.26	.07	.93	4.15	.45	.22	2.11	3.90	2.13	.31	.14	.10
21–30	.80	.33	4.09	3.99	2.34	.00	.66	.63	.00	.49	.77	.18	5.66
Total	1.66	1.61	5.99	4.92	7.19	3.25	2.99	3.27	5.88	2.84	4.53	2.43	6.90
May:													
1–10	.26	.02	1.92	.29	1.19	.00	2.01	2.04	1.98	1.96	.90	1.32	.79
11–20	.77	.82	.54	.46	.39	1.60	.66	3.24	1.13	1.88	.57	1.32	1.23
21–31	1.13	.09	.57	1.02	2.56	1.03	1.15	.66	2.43	2.03	1.36	.16	2.21
Total	2.16	.93	3.03	1.77	4.14	2.63	3.82	5.94	5.54	5.87	2.83	2.80	4.23
June:													
1–10	.00	1.04	.00	.42	.66	.53	3.33	.38	.87	.14	1.91	.18	.61
11–20	.04	.52	3.25	1.13	3.02	.36	.31	2.11	.66	1.34	1.26	.77	6.31
21–30	1.73	.89	.34	2.28	2.61	.35	.99	.26	.85	.76	.38	1.37	1.47
Total	1.77	2.45	3.59	3.83	6.29	1.24	4.63	2.75	2.38	2.24	3.55	2.32	8.39
July:													
1–10	2.83	1.56	.48	.07	1.99	5.38	5.11	1.07	3.07	.59	2.79	1.01	2.63
11–20	.32	2.56	.60	2.35	.74	.00	1.71	.97	.50	.07	.80	.17	2.05
21–31	3.55	.65	.33	.00	.14	1.11	.56	.22	4.78	1.52	.41	2.53	.08
Total	6.70	4.77	1.41	2.42	2.87	6.49	7.38	2.26	8.35	2.18	4.00	3.71	4.76
August:													
1–10	1.12	.54	.07	.89	.90	.00	.76	1.69	.05	.32	.80	.28	.73
11–20	.85	3.70	2.43	11.72	.00	.12	3.22	.56	1.81	1.30	.37	.08	1.44
21–31	.65	2.37	3.06	1.15	.45	.04	6.11	.05	8.20	.49	1.08	3.60	5.13
Total	2.62	6.61	5.56	13.76	1.35	.16	10.09	2.30	10.06	2.11	2.25	3.96	7.30
September:													
1–10	.62	2.48	1.85	2.10	1.33	.22	.43	2.94	.49	4.34	8.00	.10	1.40
11–20	.92	.0	.44	1.47	1.28	.58	.32	.00	.97	5.29	.08	.15	.26
21–30	.23	1.61	.00	.74	1.10	.00	1.23	1.17	.68	1.04	.28	2.32	.44
Total	1.77	4.09	2.29	4.31	3.71	.80	1.98	4.11	2.14	10.67	8.36	2.57	2.10
Total for 6 months	16.68	20.46	21.87	31.01	25.55	14.57	30.89	20.63	34.35	25.91	25.52	17.79	33.68

TABLE 2.—*Rainfall at Florence, S. C., for 10- and 11-day periods during the growing seasons, 1933–36*

Month and date	Rainfall during growing season for—				Month and date	Rainfall during growing season for—			
	1933	1934	1935	1936		1933	1934	1935	1936
April:	*In.*	*In.*	*In.*	*In.*	July:	*In.*	*In.*	*In.*	*In.*
1–10	0.05	0.46	1.12	6.70	1–10	1.01	0.40	1.40	0.35
11–20	1.33	.61	.59	.00	11–20	1.86	2.47	.96	1.10
21–30	.12	.00	.81	.24	21–31	3.83	1.19	3.13	1.73
Total	1.50	1.07	2.52	6.94	Total	6.70	4.06	5.49	3.18
May:					August:				
1–10	1.47	.00	.30	.05	1–10	.10	.76	.05	2.74
11–20	.00	3.64	1.40	.00	11–20	.88	.35	.91	.17
21–31	3.24	1.52	.26	.12	21–31	.04	2.27	3.66	1.21
Total	4.71	5.16	1.96	.17	Total	1.02	3.38	4.62	4.12
June:					September:				
1–10	1.24	1.36	.60	1.54	1–10	2.30	1.62	5.57	1.47
11–20	1.24	.16	.66	4.82	11–20	.00	1.25	.77	2.88
21–30	1.42	2.30	.00	.51	21–30	.00	.76	.64	1.93
Total	3.90	3.82	1.26	6.87	Total	2.30	3.63	6.98	6.28
					Total for 6 months	20.13	21.12	22.83	27.56

The effects of natural weed fallow and bare fallow on acre yields, gross value, and average price per pound of tobacco (table 3) represent a continuation and extension of previously published data (*1*). The earlier years (1922–24) are not reported again, since it is desired to point out in the present paper the advantage of weed fallow as compared to bare fallow. The results presented are for the years 1925–37, which is the period in which a direct comparison was made between bare and natural weed fallow. Period averages are presented to show trends under the two systems.

TABLE 3.—*Effects of vegetation cover on the yield, gross value, and average price per pound of leaf tobacco, Upper Marlboro, Md., 1925–37*

[1,000 pounds per acre of 1-7-5 fertilizer used in 1925–33; 750 pounds per acre of 2-8-12 fertilizer in 1934–37]

Treatment	Acre yield									
	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934
2-year rotation:	*Pounds*	*Pounds*	*Pounds*	*Pounds*	*Pounds*	*Pounds*	*Pounds*	*Pounds*	*Pounds*	*Pounds*
Weed fallow	1,264	1,152	1,504	1,080	1,204	1,064	936	1,224	1,180	1,500
Bare fallow	1,328	1,144	1,374	768	900	776	696	928	688	740
3-year rotation:										
Weed fallow	1,344	1,268	1,488	1,168	1,192	1,080	1,024	1,548	1,064	1,588
Bare fallow	1,412	1,240	1,380	800	916	784	636	948	544	933
	Acre value									
2-year rotation:	*Dollars*	*Dollars*	*Dollars*	*Dollars*	*Dollars*	*Dollars*	*Dollars*	*Dollars*	*Dollars*	*Dollars*
Weed fallow	426	415	426	328	503	230	271	317	295	410
Bare fallow	458	389	318	198	276	111	92	82	74	58
3-year rotation:										
Weed fallow	456	441	429	390	431	185	308	418	346	531
Bare fallow	487	435	329	333	243	122	67	96	65	82

Treatment	Acre yield							Average price per pound			
	1935	1936	1937	1925–28	1929–32	1933–37	1925–37	1925–28	1929–32	1933–37	1925–37
2-year rotation:	*Lb.*	*Lb.*	*Lb.*	*Lb.*	*Lb.*	*Lb.*	*Lb.*	*Cents*	*Cents*	*Cents*	*Cents*
Weed fallow	1,220	1,098	920	1,250	1,107	1,184	1,180	------	------	------	------
Bare fallow	784	720	696	1,154	825	726	888	------	------	------	------
3-year rotation:											
Weed fallow	1,040	1,528	1,009	1,317	1,211	1,246	1,257	------	------	------	------
Bare fallow	752	888	666	1,208	821	757	915	------	------	------	------
	Acre value										
2-year rotation:	*Dollars*	*Dollars*	*Dollars*	*Dollars*	*Dollars*	*Dollars*	*Dollars*				
Weed fallow	347	311	134	399	330	299	339	32	30	25	29
Bare fallow	111	106	59	341	140	82	179	30	17	11	20
3-year rotation:											
Weed fallow	270	495	150	429	336	358	373	33	28	29	30
Bare fallow	121	130	41	396	132	88	196	33	16	12	21

The data presented in table 4 give yield and value of tobacco following pure cultures of local weeds and following bare fallow. This series differs from that shown in table 5 in that the weeds were plowed under in the fall. The plots were duplicated in most cases in the series shown in table 5. The plot numbers will indicate whether the results shown are averages of duplicate plots or were obtained from single treatments. The weed growth in this series was not plowed under until spring, usually in April.

TABLE 4.—*Acre yield, gross value, and average price per pound of leaf tobacco grown in 2-year rotation with pure cultures of the local weeds, Upper Marlboro, Md., 1931–37*

[600 pounds per acre of 2-8-12 fertilizer applied to the tobacco crop on all treatments; weeds plowed under in fall]

Treatment	Yield per acre								Average price per pound
	1931	1932	1933	1934	1935	1936	1937	Average 1931–37	
	Pounds	*Pounds*	*Pounds*	*Pounds*	*Pounds*	*Pounds*	*Pounds*	*Pounds*	*Cents*
Rabbitfoot clover	782	1,069	669	1,263	950	938	696	910	.....
Ragweed	844	1,276	831	1,175	913	976	875	984	.....
Wild pea	932	1,275	1,006	1,513	1,351	1,113	800	1,141	.....
Fallow	900	981	757	863	801	764	600	809	.....
Partridge-pea	1,100	1,264	931	1,250	1,026	988	651	1,030	.....
Horseweed	894	1,269	732	1,163	700	875	513	878	.....
Lespedeza	982	1,019	638	1,163	801	901	575	868	.....
	Value per acre								
	Dollars	*Dollars*	*Dollars*	*Dollars*	*Dollars*	*Dollars*	*Dollars*	*Dollars*	
Rabbitfoot clover	176	243	99	249	194	246	44	179	20
Ragweed	160	362	143	168	202	282	73	199	20
Wild pea	139	322	193	132	257	297	83	205	18
Fallow	173	163	59	52	115	157	33	107	13
Partridge-pea	154	281	175	242	197	226	47	189	18
Horseweed	128	360	144	251	146	241	32	186	21
Lespedeza	143	192	77	126	164	251	51	143	16

TABLE 5.—*Acre yield, gross value, and average price per pound of leaf tobacco grown in 2-year rotation with pure cultures of the local weeds, Upper Marlboro, Md., 1931–37*

[600 pounds per acre of 2-8-12 fertilizer applied to the tobacco crop on all treatments; weeds plowed under in spring]

Plot No.	Treatment	Yield per acre							Average		6-year average price per pound	5-year average price per pound
		1931	1932	1933	1934	1935	1936	1937	1931–37	1932–37		
		Lb.	*Lb.*	*Lb.*	*Lb.*	*Lb.*	*Lb.*	*Lb.*	*Lb.*	*Lb.*	*Ct.*	*Ct.*
1	Annual sweetclover (Hubam strain)	844	1,287	1,042	1,261	1,143	1,173	901	1,093	1,135	.....	.....
2, 9	Rabbitfoot clover	1,003	1,335	1,313	1,025	1,124	1,396	1,007	1,172	1,200	.....	.....
3, 10	Ragweed	1,018	1,440	1,306	1,492	1,291	1,322	1,068	1,277	1,320	.....	.....
4, 11	Wild pea	1,146	1,453	1,160	1,274	1,105	1,330	924	1,199	1,208	.....	.....
5, 12	Fallow	1,059	1,327	1,147	1,020	1,098	1,090	828	1,081	1,085	.....	.....
6, 13	Partridge-pea	1,085	1,344	1,287	1,309	1,221	1,146	950	1,191	1,210	.....	.....
7, 14	Horseweed	1,189	1,379	1,177	1,235	1,210	1,212	949	1,193	1,194	.....	.....
8	Lambsquarters	932	1,286	901	884	459	806	613	840	825	.....	.....
15	Lespedeza	1,068	1,208	1,269	963	1,090	1,174	954	1,104	1,110	.....	.....
16	Natural weed fallow	.....	1,243	1,086	1,217	1,204	1,164	929	.....	1,141	.....	.....
		Value per acre										
		Dol.	*Dol.*	*Dol.*	*Dol.*	*Dol.*	*Dol.*	*Dol.*	*Dol.*	*Dol.*		
1	Annual sweetclover (Hubam strain)	193	284	278	340	264	237	80	242	251	22	22
2, 9	Rabbitfoot clover	156	320	314	140	257	382	107	239	253	20	21
3, 10	Ragweed	161	434	409	407	375	424	143	336	365	26	28
4, 11	Wild pea	179	352	286	171	233	353	123	242	253	20	21
5, 12	Fallow	203	291	223	186	158	274	82	202	202	19	19
6, 13	Partridge-pea	222	334	350	332	265	260	119	269	277	23	23
7, 14	Horseweed	284	447	278	295	312	344	106	295	297	25	25
8	Lambsquarters	214	307	184	100	49	147	61	152	141	18	17
15	Lespedeza	247	219	181	196	179	343	102	210	203	19	18
16	Natural weed fallow	.....	392	278	294	298	334	117	.....	286	.....	25

The results presented in table 6 were obtained from tests at the Pee Dee Experiment Station, Florence, S. C. These tests covered only a

short period of time (1933–36) but were located on a soil differing from that upon which the other tests were conducted. The flue-cured type of tobacco was grown at Florence, and this type differs from that produced in the other tests, which is known as Maryland leaf.

TABLE 6.—*Acre yield, gross value, and average price per pound of leaf tobacco grown in a 2-year rotation with pure cultures of some of the local weeds at Florence, S. C., 1933–36*

[800 pounds per acre of 3-8-6 fertilizer applied to tobacco on all plots]

Treatment	Yield per acre					Average price per pound
	1933	1934	1935	1936	Average 1933-36	
	Pounds	*Pounds*	*Pounds*	*Pounds*	*Pounds*	*Cents*
Ragweed	1,758	1,873	1,877	1,330	1,710	
Partridge-pea	1,254	1,697	1,700	1,240	1,473	
Horseweed	1,698	1,650	1,653	1,308	1,577	
Lambsquarters	774	932	927	810	861	
Natural weed fallow	1,022	1,365	1,408	1,393	1,297	
	Value per acre					
	Dollars	*Dollars*	*Dollars*	*Dollars*	*Dollars*	
Ragweed	224	410	413	328	344	20
Partridge-pea	100	342	342	337	280	19
Horseweed	219	346	351	341	314	20
Lambsquarters	72	147	148	226	148	17
Natural weed fallow	115	276	297	410	275	21

The percentage of plants harvested from the several treatments shown in table 5 is given in table 7. These data serve to illustrate survival and ultimate growth of tobacco following the various plant species included in the test. The effect of bare and natural weed fallow on size, weight per square foot, percentage of moisture, and fire-holding capacity of leaf tobacco is shown in table 8. The data in this table include physical measurements of properties associated with some of the rather elusive factors of quality. One leaf of average size selected from each of 50 normal plants for the years shown was used to ascertain the size, weight per square foot, and moisture-absorbing capacity when the cured leaf is handled under controlled temperature and humidity. Fire-holding capacity was determined on 50 leaves selected and handled in the same manner.

TABLE 7.—*Percentage of the tobacco plants harvested on each treatment when the crop was grown in 2-year rotation with pure cultures of local weeds, Upper Marlboro, Md., 1931–37*

Plot No.	Treatment	1931	1932	1933	1934	1935	1936	1937	Average	
									1931–37	1932–37
		Per-cent	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*
1	Annual sweetclover (Hubam strain)	100	100	100	92	97	100	100	98	98
2, 9	Rabbitfoot clover	97	100	100	91	99	100	97	98	98
3, 10	Ragweed	100	100	100	95	100	99	100	99	99
4, 11	Wild pea	100	100	91	95	91	100	91	95	95
5, 12	Fallow	100	100	100	95	100	100	100	99	99
6, 13	Partridge-pea	100	100	100	97	100	100	100	100	100
7, 14	Horseweed	100	100	93	100	100	97	100	99	98
8	Lambsquarters	100	100	83	71	54	67	76	79	75
15	Lespedeza	100	100	100	83	96	79	100	94	93
16	Natural weed fallow	------	100	100	100	100	90	97	------	98

TABLE 8.—*Effects of bare and natural weed fallow on amount of moisture, size, weight per square foot, and fire-holding capacity of leaf tobacco*

Treatment	Amount of moisture in the leaf, 1935	Average size of leaf				
		1929	1931	1932	1935	Average
2-year rotation:	*Percent*	*Square feet*	*Square feet*	*Square feet*	*Square feet*	*Square feet*
Weed fallow	21.85	1.19			1.10	1.15
Bare fallow	19.43	.75			.67	.71
3-year rotation:						
Weed fallow	21.16	.99	1.67	1.49	1.19	1.34
Bare fallow	19.75	.92	1.02	.88	.75	.89

Treatment	Weight per square foot					Fire-holding capacity				
	1929	1931	1932	1935	Average	1929	1931	1932	1934	Average
2-year rotation:	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Seconds*	*Seconds*	*Seconds*	*Seconds*	*Seconds*
Weed fallow	6.05			5.84	5.95	13.5	47.3	16.9	55.8	33.4
Bare fallow	9.22			7.70	8.46	5.4	17.8	12.0	28.9	16.0
3-year rotation:										
Weed fallow	6.83	4.27	7.28	5.99	6.09	9.9	50.2	14.3	71.0	36.4
Bare fallow	7.90	5.16	8.78	7.26	7.28	6.5	23.0	12.0	22.0	15.9

DISCUSSION

Successful culture of tobacco does not depend simply on the tonnage produced per acre, for the product must meet market demands as to color, aroma, texture, elasticity, body, fire-holding capacity, ability to undergo the aging process with improvement, and other requisites of quality. These diverse and exacting demands can be met only by close attention to details of culture and handling. It is not uncommon for the grower to observe all precautions known to him in regard to these details and yet fail to produce high-quality leaf, owing to the use of undesirable soil, improper cropping systems, inadequate fertilization, the invasion of parasites, and other causes not well understood.

A system that consistently gives good yields of high-quality leaf is always worthy of consideration. It is clearly evident from the data presented in table 3 that high-quality leaf was consistently produced when the tobacco was grown after a natural weed fallow. The crop that followed bare fallow decreased in value until the returns did not defray the cost of production. It is evident that in the earlier years of the test the portions of the plots that were kept bare produced as high crop yields and values as the portions on which the weeds were allowed to grow. The yields and values were maintained under the 3-year system, while the 2-year system showed some falling off though not to any great extent. It is possible that there was an improvement under the 3-year weed rotation, since the top prices paid for Maryland leaf tobacco were much higher during the earlier years of the test than those prevailing in recent years. The yields per acre remained at the same high level of about 1,200 pounds per acre under both the 2- and 3-year systems. The values appear to have fallen off under the 2-year system, since the average of the first 4 years was somewhat higher than that for the last 5 years. The total gross value following the 3-year system of natural weed fallow was

above $350 per acre for the last 5-year period, which is to be regarded as exceptionally good. Only in the very dry year of 1930 and the very wet years of 1935 and 1937 were the values materially reduced after natural weed fallow. The average price per pound, which serves as a good index of quality, appears to have fallen off in the 2-year system but was maintained at a high level for the tobacco grown in the 3-year system.

The relative merits of some of the wild species commonly occurring in the natural weed fallow as a cover crop for tobacco are well illustrated in table 4. It is evident that all of the species used resulted in increases in yield as compared to bare fallow, when the average for the period is considered. The poorest results obtained in this series were those with lespedeza. The highest gross values per acre were obtained from wild pea, with ragweed a close second. In some seasons the plot with horseweed as the cover crop produced tobacco that showed a high gross value per acre, and the average price per pound from this treatment was slightly higher than from any others. The yields and values obtained in this series, in which the weeds were plowed under in the fall, were lower than where the weed cover was allowed to remain on the soil until spring. It is possible that wind and water erosion was largely responsible for these differences.

Where spring plowing was practiced the highest yields in the series (table 5) were obtained from the ragweed cover. This plot also produced the highest gross value per acre and the highest average price per pound. It is significant that the next highest gross value and average price per pound were obtained from the plot with horseweed as the preceding cover. Natural weed fallow followed horseweed in gross value of tobacco produced and gave the same average price per pound for the tobacco as that obtained from the horseweed plot. In contrast with these results, reduction in yield and value occurred on the plot where lambsquarters was the cover crop (fig. 1), as compared to bare fallow. There also appears to have been no advantage from lespedeza as a cover crop, since the yield and value of the leaf produced was almost the same as on bare fallow. Sweetclover, rabbitfoot clover, and wild pea did not always show a decided advantage as cover crops to precede tobacco in this series. Partridgepea appears to have produced some increase in yields and values as compared with bare fallow.

The chief virtue of the weed cover for the succeeding tobacco crop appears to be its effect in inducing a rapid and uniform growth of tobacco from transplanting time to maturity. The tobacco following ragweed (fig. 2) serves as a good example of this effect. In those cases in which the plants do not grow uniformly, as with the lambsquarters (fig. 1) and lespedeza (fig. 3), the stunted plants as a rule show no very definite symptoms under Maryland conditions except those associated with brown root rot. Under South Carolina conditions, when tobacco follows lambsquarters, nematodes often are the most apparent cause for failure of the tobacco plants to grow. It is possible that the inhibitory growth factors not yet indentified are the same in both instances and that the two visible causes, brown root rot and nematodes, are only secondary invaders. It has been observed in the case of tobacco following annual lespedeza under Maryland conditions that seemingly the failure to grow uniformly

FIGURE 1.—Tobacco following (*A*) lambsquarters, and (*B*) horseweed. Upper Marlboro, Md., August 16, 1935. (See table 5 for yields and values.)

FIGURE 2.—Tobacco following (*A*) common ragweed, and (*B*) wild pea. Weeds in background. Upper Marlboro, Md., July 20, 1933. (See table 5 for yields and values.)

FIGURE 3.—Tobacco following (*A*) annual lespedeza, and (*B*) horseweed. Upper Marlboro, Md., September 6, 1934. (See table 5 for yields and values.)

and rapidly is due to brown root rot. Tobacco following lespedeza in some locations frequently shows a heavy invasion of nematodes, while in other locations black root rot (*Thielaviopsis basicola* (B. and Br.) Ferraris) is the most evident cause for failure of the crop to develop normally. Again, the most apparent causes may be only secondary.

While the tests conducted in South Carolina were not so extensive and were not continued for so long a period as those in Maryland, the results secured were nonetheless positive (table 6). Highest yields and values were obtained where ragweed was grown as the preceding cover (fig. 4, *A*). Horseweed gave results that were almost as good as those obtained from ragweed (fig. 4, *B*). The poorest yields and values obtained in the South Carolina tests were from lambsquarters (fig. 4, *C*). Natural weed fallow and partridge-pea, as preceding cover for tobacco, produced, as a rule, high yields and values. Under South Carolina conditions the highest average price per pound was obtained from the natural-weed-fallow combination.

The low yield from lambsquarters was the result, at least in part, of the loss of many plants (table 7) that were stunted in early growth and did not reach sufficient size for harvesting, while the low value can be attributed largely to irregular maturing of the crop because of the stunting. The same situation applies to a greater or less extent to tests with annual lespedeza and some of the other legumes represented in these experiments. The differences in growth following lambsquarters and horseweed are not the result of varying amounts of plant material turned under, since the amount in each case was approximately the same (fig. 5). Differences in the quantity of organic material would appear not to be the explanation for differences in growth of tobacco following the various species.

It is significant that natural weed fallow consisting of adventitious vegetation of 2 years' duration has consistently maintained yields and values of tobacco following this weed cover. The explanation is not evident, but it is clear that this effect is not due simply to allowing the land to lie idle since in bare fallowing the crop has decreased in yield and value. In an effort to learn something as to the factors involved, in 1935 one-half of the bare-fallow plot of the 2-year rotation was covered in the fall (September 25) with weeds harvested from old fields from soils of the Collington series. These weeds were removed in the spring of 1936 prior to preparing the land for tobacco. On one-half of the bare-fallow portion of the 3-year rotation, weeds harvested the fall before and stored under cover until spring were plowed under when the land was prepared for tobacco. The actual quantities used were not determined, but an attempt was made to supply approximately the same quantity of vegetation as was growing on the natural weed-fallow plots. The results are shown in table 9. The data indicate that a vegetation cover over winter seems to be necessary for favorable effects. When plowed in the spring, the soil under the weed fallow and weed mulch over winter was more friable and moist than that on bare-fallow areas. It may be pointed out that where excessive pasturing of livestock is practiced the favorable effects reported from natural weed fallow would not be expected since the field would then tend to approach the bare-fallow conditions.

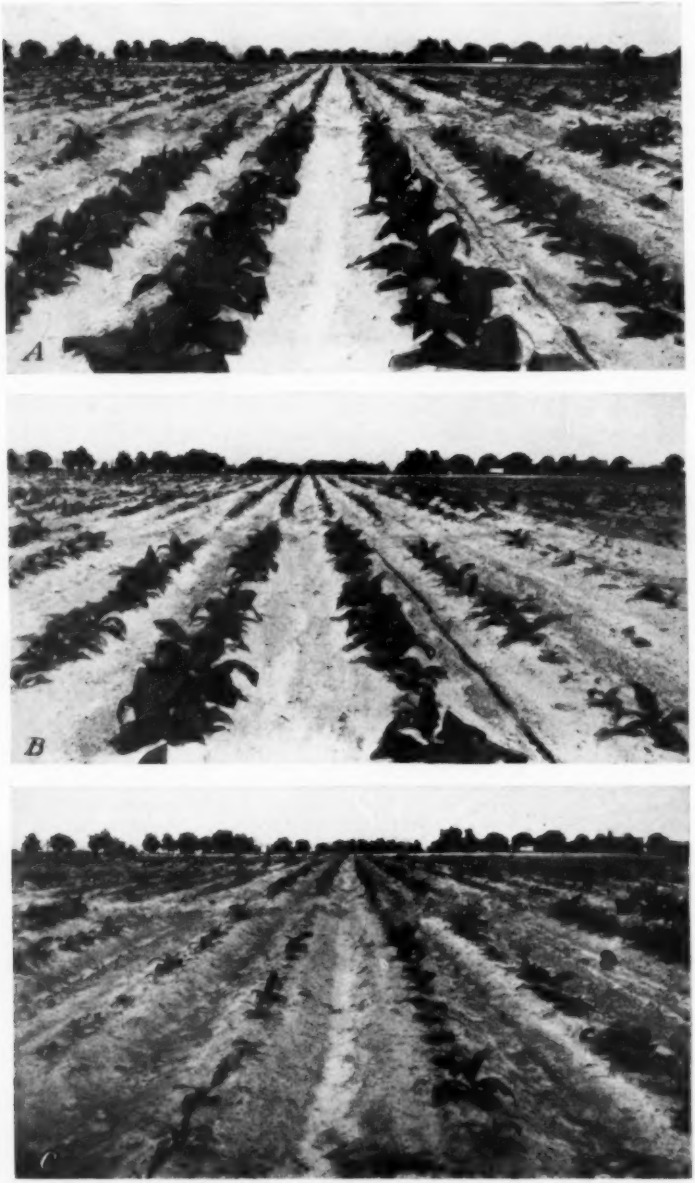

FIGURE 4.—Tobacco following (*A*) common ragweed, (*B*) horseweed, and (*C*) lambsquarters. Pee Dee Experiment Station, Florence, S. C., June 12, 1936. (See table 6 for yields and values.)

TABLE 9.—*Effect of a weed mulch, and of weeds plowed under in the spring, on yield and value per acre of tobacco, Upper Marlboro, Md., 1936*

Treatment	Yield per acre	Value per acre	Treatment	Yield per acre	Value per acre
2-year rotation:	*Pounds*	*Dollars*	3-year rotation:	*Pounds*	*Dollars*
Bare fallow	720	106	Bare fallow	888	130
Weed mulch over winter	1,080	339	Spring application of weeds	760	116
Natural weed fallow	1,098	311	Natural weed fallow	1,528	495

The tobacco crop may not under all conditions be grown to better advantage after natural weed fallow. In some instances complicating diseases such as bacterial wilt and nematodes are harbored by the prevailing weed growth. The light thin-bodied leaf (table 8) produced as a rule following natural weed fallow, is not suitable for all tobacco-manufacturing purposes. Certain economic relations are

FIGURE 5.—*A*, Growth of horseweed; *B*, comparative growth of lambsquarters, Upper Marlboro, Md., August 17, 1931.

to be considered, since in some districts good tobacco soils are scarce and high-priced. It appears, however, that the natural weed-fallow system can be used to advantage where the necessary land is available, a light-bodied leaf is desired, and there are no complicating disease relationships. The beneficial action of the natural weed fallow, especially when combined with intelligent fertilization of the tobacco crop, is reflected in a uniformly high market value per acre and average price per pound, which shows that the product meets current demands for most manufacturing purposes.

A leaf of larger size, with a higher moisture-absorbing capacity and a lighter weight per square foot, is produced on the weed-fallow plot than on the bare-fallow area (table 8). The weight per square foot may be said to represent the so-called body factor, which is so often used in the industry in describing one of the essentials of quality. Weight per square foot varies widely from season to season. This variation appears to be associated with rainfall, since light weight per square foot is definitely related to wet season and more particularly to ample and well-distributed rainfall in July and August.

The fire-holding capacity of leaf tobacco (table 8) is important if it is to be used for smoking purposes. This is particularly true of

Maryland tobacco, since its reputation has been built up largely on its good burning qualities. It is evident that the natural weed fallow has produced leaf tobacco showing a much higher fire-holding capacity than bare fallow, although there is the usual variation from season to season, due, in part at least, to variations in rainfall.

SUMMARY

Since it had been observed that high-quality tobacco was consistently produced for the first year or two after a growth of natural weed cover, experiments were initiated to determine the value of natural weed fallow for preceding tobacco in the rotation as compared with that of certain crop plants and some of the wild species commonly occurring in the natural weed fallow. These comparisons were based on bare fallow as a control.

It is clearly evident from the results herein presented that tobacco which is fertilized intelligently and grown after natural weed fallow of sufficient duration possesses in large measure those desirable characteristics that are observed in the crop grown on virgin land. The crop grown after bare fallow has shown a rapid decline in yield and gross value.

The tests conducted with individual weed and crop-plant species have consistently shown that certain species are much more desirable than others as cover crops to precede tobacco. Tobacco following ragweed and horseweed was markedly superior both in yield and value to that following bare fallow. On the other hand, tobacco following lambsquarters was inferior in yield and value to that following bare fallow. In these tests annual lespedeza has shown no advantage as a cover crop to precede tobacco; sweetclover, rabbitfoot clover, and wild pea have not always shown a decided advantage; while partridge-pea has produced some increase in yield. Although the natural weeds occurring in these tests consisted principally of species that produced high-quality leaf in pure stands, it is possible that those found to be objectionable might predominate, under some conditions, with a resulting harmful effect on the succeeding tobacco crop. It is hardly to be expected that a given weed species would have the same effect on tobacco on all soils or under all conditions.

The generally beneficial effect of the weed fallow was that it promoted a quick start and very rapid and uniform growth of the tobacco plants from transplanting time to maturity. Within normal limits this result is, in turn, associated with a uniformly high market value per acre and average price per pound.

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A STUDY OF HYBRID VIGOR IN A CROSS BETWEEN POLAND CHINA AND DUROC JERSEY SWINE[1]

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INTRODUCTION

Cross-breeding has been used for the purpose of recombining the best characteristics of two or more breeds in the formation of a new breed. This is a process that requires many years of continued selection. A second purpose in cross-breeding is to obtain immediate offspring possessing more desirable characteristics, such as greater size, more economical feed utilization, or more rapid growth, than are exhibited by either parental breed.

Interest in cross-breeding for the production of market animals has been of long duration and at the present time is greater in the United States than it has been for decades. The recent success in the production of hybrid corn may have been a stimulating factor in this interest.

The purpose of this experiment was to study the effect of cross-breeding on weight of pigs at birth, vigor, rapidity of growth, and economy of gain.

BREEDS AND METHODS

Duroc Jersey and Poland China breeds were used. Double matings were made according to the following system:

$$\text{Duroc Jersey sow} \times \begin{cases} \text{Duroc Jersey boar} \\ \text{Poland China boar} \end{cases}$$

$$\text{Poland China sow} \times \begin{cases} \text{Duroc Jersey boar} \\ \text{Poland China boar} \end{cases}$$

The two boars were usually mated to the same sow with as little time elapsing between the two services as possible. The same two boars in any one season were mated to all sows. The order of service of the two boars was alternated in order to eliminate the possibility of order of mating affecting the kind of offspring produced.

During gestation the sows were given similar feed and care which were considered to be adequate. After farrowing. the mothers and litters were handled in accordance with the McLean County swine-sanitation system, all receiving similar feed and care.

All pigs were weighed and given individual earmarks at birth, later immunized against hog cholera, and the boar pigs castrated. At weaning or soon thereafter the pigs were separated into the following groups: Purebred Duroc Jersey; purebred Poland China; crossbred pigs from Duroc Jersey female × Poland China male; and crossbred pigs from Poland China female × Duroc Jersey male.

The various groups of pigs were fed, in dry lots, shelled corn and a protein supplemental mixture in separate compartments of self-feeders. The supplemental mixture consisted of 2 parts tankage, 1

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part linseed meal, and 1 part alfalfa meal. The pigs were kept on this ration until they reached an approximate weight of 200 pounds.

Weights of pigs were taken at birth, when put into lots, and every 2 weeks thereafter until final weight was reached. Records of feed consumption by groups were also kept.

TABLE 1.—*Relation of time elpasing between services in double-mated sows and parentage of litters*

Interval between services (minutes)	Matings	Litters sired by—			Interval between services (minutes)	Matings	Litters sired by—		
		First boar only	Second boar only	Both boars			First boar only	Second boar only	Both boars
	Number	*Number*	*Number*	*Number*		*Number*	*Number*	*Number*	*Number*
1	12	3	1	8	15	1	0	1	0
2	22	1	5	16	18	1	0	0	1
3	9	3	0	6	20	1	0	0	1
4	10	2	2	6	25	1	0	1	0
5	12	3	2	7	240	1	1	0	0
6	5	2	0	3	480	1	0	1	0
7	1	0	1	0	540	1	0	1	0
8	2	2	0	0	720	1	0	1	0
10	3	1	1	1	960	1	1	0	0
12	1	0	0	1	Total	86	19	17	50

EFFECT OF TIME BETWEEN SERVICES ON PARENTAGE OF YOUNG

The time elapsing between services by the two boars varied from 1 minute to 16 hours, though the majority of double matings were made within a 6-minute interval (table 1). The litter produced in the case of the 16-hour interval was sired entirely by the first boar. The next longest time elapsing between services, was 12 hours, in which case the pigs were from the second boar. The single litters[2] were sired with approximately equal frequency by the two boars regardless of the time interval, at least up to 12 hours. Nor does the interval between services appear to affect the parentage of pigs in mixed litters.[2] However, a greater proportion of mixed litters resulted from matings with short intervals between services than from those in which the intervals were longer. Among 65 double matings with intervals between services of 5 minutes or less 43 mixed litters were produced. Among 15 litters with intervals of 6 to 20 minutes inclusive between services only 7 were mixed. No mixed litters were produced in 6 cases in which the interval between services was longer than 20 minutes.

ORDER OF MATING IN RELATION TO PARENTAGE OF PIGS

The order of mating within the time elapsing between services (table 1) had no significant relation to the parentage of the pigs produced. Among 40 litters with only 1 sire represented in a litter,[3] the boars used first produced 21 and the boars used last produced 19

[2] The three kinds of litters produced from double matings are designated as follows: Purebred litter, a litter all pigs of which were sired by the boar of the same breed as that of the sow; crossbred litter, a litter all pigs of which were sired by the boar of the breed different from that of the sow; mixed litter, a litter containing pigs sired by both boars; single litter, a litter all pigs of which were sired by one boar, and may be either purebred or crossbred.

[3] In table 1 only 36 litters sired by one boar are shown because the time between services was not recorded for the remaining matings.

litters. However, there was a greater number of litters with all pigs either purebred or crossbred than would be expected on the basis of random fertilization with two kinds of spermatozoa present in equal numbers. The proportions among 105 litters where double mating was used were 24 purebred, 16 crossbred, and 65 mixed litters.

Two possible explanations of this unexpected distribution are: (1) The spermatozoa of the two boars were deposited in different positions in the reproductive tract. Those deposited closer to the oviduct, and consequently to the eggs, would have the first opportunity of fertilizing the eggs. (2) Variation in the relative fertility of the two boars at different services.

While the kinds of litters were not influenced by the order of mating, the kinds of pigs in mixed litters were affected by the order of mating (table 2). In 65 mixed litters containing 637 pigs, 359 were sired by the boar used first and 278 by the boar used last. Assuming numbers of sperm and other conditions to be similar, with random fertilization a ratio of 1:1 in respect to the offspring of the two would be expected. The observed results deviate 40.5 from the expected. The probable error of this ratio is 8.5. $\frac{D}{PE}=4.8$, and indicates a significant departure from the expected. With all litters, both single and mixed, the boars used first sired 546 pigs and those used last sired 402.

Among 637 pigs in the 65 mixed litters, 329 were purebred and 308 were crossbred. The deviation here is 10.5 and $\frac{D}{PE}=1.2$, indicating a close fit to the theoretical expectation. In the matings to produce these 65 litters, boars which would produce purebred pigs were used first 35 times and boars which would produce crossbred pigs were used first 30 times. Since according to these figures, the boars used first have a greater chance of being parents than the boars used last, a correction can be made. On the basis of the foregoing results the first boar has a chance of 359/637 of being the sire of a given pig. Correcting for the five extra matings of boars which would produce purebreds, the ratio becomes 325.8 : 311.2. $\frac{D}{PE}=0.86$, indicating a very close fit to the theoretical expectation.

TABLE 2.—*Number of litters and pigs produced by the first and the second boar*

Matings			Single litters sired by—				Mixed litters sired by both boars		
			First boar		Second boar			Pigs from—	
First boar	Second boar	Sow	Litters	Pigs	Litters	Pigs	Litters	First boar	Second boar
			Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
Duroc Jersey	Poland China	Duroc Jersey	2	16	5	35	15	104	72
Poland China	Duroc Jersey	do	5	53	4	20	14	77	56
Do	do	Poland China	10	95	2	7	20	101	82
Duroc Jersey	Poland China	do	4	23	8	62	16	77	68
Total			21	187	19	124	65	359	278

AGE OF BOAR AND NUMBER OF PIGS PRODUCED

Thirteen mixed litters with 125 pigs were produced by double matings in which the boars used first were at least 1½ years older than the boars used last. The first boar sired 62 pigs and the second 73. Sixteen mixed litters with 170 pigs were produced in which the boars used first were at least 1½ years younger than those used last. In this case the first boars sired 103 pigs and the second 67. In mixed litters from boars of the same age (±3 months) 195 pigs were sired by the first boar and 138 by the second. These figures indicate that younger boars tend to produce more pigs in mixed litters than do older boars but, other things being equal, when two boars are used in double matings more pigs are likely to be sired by the first boar than by the second.

SIZE OF SINGLE LETTERS AS COMPARED WITH MIXED LITTERS

The mean litter size of 40 single litters from double matings was 7.78±.36, whereas in 65 mixed litters with two sires the litter size was 9.82±.24, a significant difference. $D=2.04\pm.43$. The age of the dam, however, influences the size of the litter. The average age of the mothers of the 40 single litters was 1.88 years, and that of the mothers of the 65 mixed litters, 2.14 years. In order to eliminate the effect of age, 40 mixed litters were taken whose mothers were of the same ages as the mothers of the single litters. The results were still significantly in favor of the litters from two males being larger than litters from single males. With the ages the same, the average size of litters with two sires was 9.70±.26. The difference between this and the size of single litters is 1.92±.44. $\frac{D}{PE}=4.36$. The exact cause of this difference is not evident. That it is not due to a higher intrauterine survival of crossbred pigs is indicated by the fact that the 24 purebred single litters had an average litter size of 8.0, while 16 crossbred litters had an average size of 7.4. In these averages, age of sows was not considered, but when only sows of the same ages are used in the computations the average litter sizes for purebreds and crossbreds are 7.4 and 7.0, respectively.

BIRTH WEIGHTS OF PUREBRED AND CROSSBRED PIGS

Birth weights of purebred and crossbred pigs were analyzed in three different ways, taking:

(1) All pigs whether born in single or mixed litters.
(2) The average weight of purebred and of crossbred pigs of the same sex in mixed litters. The average weight of purebreds in a mixed litter was paired with the average weight of the crossbreds and analyzed by Student's method.
(3) Pairs consisting of a purebred and a crossbred pig of the same sex taken at random from each mixed litter and analyzed by Student's method.

By the first method in which all purebred pigs were compared with all crossbred pigs, no significant difference between purebreds and crossbreds was found. The mean birth weight of purebred was 2.62±.02 pounds and that of the crossbreds was 2.64±.02.

When the average birth weights of purebred and crossbred pigs of the same sex and litter were compared the only significant difference found was between purebred and crossbred females from Poland China

sows × Poland China and Duroc Jersey boars. In this case the average weight of the purebreds was 2.61±.05 and of the crossbreds 2.90±.06 (table 3). For all purebreds and crossbreds in these mixed litters, the average birth weight of the purebreds is 2.62±.03 and for the crossbreds 2.72±.03. The difference is 0.10±.04, which is not significant.

The third method of analysis was to take pairs, one member of a pair purebred and the other a crossbred of the same sex from the same litter. These pairs were taken at random and the total number was 184. The mean difference is 0.1299 pound in favor of the crossbreds and the value of P is 0.9793. The odds are 194 to 1 in favor of the crossbreds. The average birth weights in pounds of the purebreds and crossbreds in these pairs are 2.63 and 2.76, respectively.

TABLE 3.—*Comparison of average birth weights of purebred and crossbred pigs in mixed litters by parentage and sex*

Mating			Males			Females		
First boar	Second boar	Sow	Pairs of averages	Purebred	Crossbred	Pairs of averages	Purebred	Crossbred
			Number	*Pounds*	*Pounds*	*Number*	*Pounds*	*Pounds*
Duroc-Jersey	Poland China	Duroc-Jersey	22	2.55±.084	2.74±.060	22	2.56±.070	2.55±.052
Do	do	Poland China	29	2.73±.065	2.68±.073	28	2.61±.052	2.90±.060

STRENGTH OF PIGS AT BIRTH

At farrowing the pigs were classified in respect to strength as strong, medium, weak, and dead except for those in seven litters early in the experiment. On the basis of the appearance and activity of the pigs at birth 3.7 percent more of the crossbreds than of the purebreds were graded strong and also 2.4 percent less of the crossbreds were in the medium class (table 4). The percentage of weak pigs was slightly higher for purebreds, though the percentage of purebreds farrowed dead was lower.

MORTALITY BEFORE VACCINATION

The average age at which the pigs were vaccinated was 38 days. Owing to the presence of some undiagnosed disease in the herd, mortality was exceptionally high one year. In mixed litters (table 5) the mortality of the crossbred pigs was 39.6 percent while that of the purebreds was 48.6 percent. In single litters the mortality was greater in the crossbreds than in the purebreds by 10.7 percent. When all purebred and crossbred pigs are considered, the mortalities in percent are 43.3 and 41.1, respectively.

RESULTS OF FEEDING TESTS

Purebred and crossbred pigs from different dams were not included in the feeding trials, except in one instance, because environmental differences among such pigs are greater than among purebred and crossbred pigs farrowed in the same litter. Such environmental

differences might mask the real effects of cross-breeding. Feeding tests were conducted with only 3 of the 5 crops of pigs. While there were 65 mixed litters at weaning time, the number for 2 years, containing both purebred and crossbred pigs, was considered too small for reliable feeding tests. For this reason only 20 mixed litters were available for the feeding trials.

TABLE 4.—*Strength at birth of purebred and crossbred pigs farrowed in mixed litters*

Condition of new-born animal	Purebred		Crossbred	
	Number	*Percent*	*Number*	*Percent*
Strong	195	68.5	200	72.2
Medium	40	14.0	32	11.6
Weak	36	12.6	28	10.1
Dead	14	4.9	17	6.1
Total	285	100.0	277	100.0

TABLE 5.—*Number and percentage of pigs alive at vaccination at an average age of 58 days*

Born in—	Pigs farrowed		Pigs alive at vaccination			
	Purebred	Crossbred	Purebred		Crossbred	
	Number	*Number*	*Number*	*Percent*	*Number*	*Percent*
Mixed litters	329	308	169	51.4	186	60.4
Single litters	193	118	127	65.8	65	55.1
Total	522	426	296	56.7	251	58.9

Initial weights, average daily gains, and final weights obtained from the feeding trials may be analyzed in various ways. The averages of these measurements for purebreds and crossbreds may be compared directly by including all purebreds and crossbreds used in the experiment (tables 6 and 7). A more critical analysis may be made by comparing the average of the purebreds with that of the crossbreds in each litter. By this method many environmental factors which might otherwise disturb the results are eliminated. The members of the pair have the same mother and have been subjected to the same maternal conditions, which are known to be important. They are of the same age when put into the feed lots. Table 8 gives the results of the statistical analysis of pairs of averages from 20 litters. These pairs were analyzed by Student's method.

The average initial weight of the purebred pigs from the 20 mixed litters as the pigs were started on the feeding trial portion of the experiment was 65.3 pounds. The average weight of the crossbred pigs of the same litters at the same time was 68.4 pounds. The difference is not significant.

The daily rates of gain for averages of purebreds and crossbreds were 1.59 and 1.65 pounds, respectively, again not significantly different.

While on the feeding tests the animals were in groups according to parentage and, therefore, the individual feed consumption is not available. The feed consumption by lots of purebreds and crossbreds is given in tables 6 and 7. The amount of feed consumed per unit of gain in two of the three feeding trials was in favor of the crossbreds

and one was in favor of the purebreds. If all purebreds are compared with all crossbreds the feed consumption per 100 pounds of gain was 409 pounds for the purebreds and 402 for the crossbreds. This is not a significant difference.

TABLE 6.—*Weights, gains, and feed consumption of purebred and crossbred pigs for 3 years, 1925, 1927, and 1929*

Item	1925				From mixed litters, 1927				From mixed litters, 1929			
	Purebred litter	Purebreds from mixed litters	Crossbreds from mixed litters	Crossbred litter	Purebred Duroc Jerseys	Crossbreds by Duroc Jersey sire	Crossbreds by Poland China sire	Purebred Poland Chinas	Purebred Duroc Jerseys	Crossbreds by Duroc Jersey sire	Crossbreds by Poland China sire	Purebred Poland Chinas
Pigs started ....number	7	5	15	7	8	12	4	18	16	13	14	13
Pigs finished .... do	6	5	14	7	8	11	4	18	15	13	14	13
Average age at start..days..	75	77	78	78	111	107	112	109	130	130	131	132
Average time required to finish.....days..	96	102	94	85	98	98	63	84	71	71	77	77
Average initial weight pounds..	51	39	47	55	60	64	96	72	67	72	67	72
Average final weight pounds..	204	200	205	205	203	202	208	198	196	200	204	197
Average daily gain pounds..	1.59	1.57	1.68	1.77	1.45	1.38	1.79	1.50	1.79	1.80	1.78	1.62
Feed consumed per 100 pounds of gain pounds..	391	401	378	400	423	422	406	427	389	398	411	410

TABLE 7.—*Summary of weights, gains, and feed consumption of purebred and crossbred pigs for 3 years, 1925, 1927, and 1929*

Item	1925		1927	
	Purebred	Crossbred	Purebred	Crossbred
Pigs.....number	11	21	26	15
Average initial weight.....pounds..	47	53	69	70
Average time required to finish.....days..	99	91	88	89
Average daily gain.....pounds..	1.59±.031	1.71±.018	1.49±.055	1.50±.055
Feed consumed per 100 pounds of gain....do....	396	385	426	418

Items	1929		Totals	
	Purebred	Crossbred	Purebred	Crossbred
Pigs.....number..	28	27	65	63
Average initial weight.....pounds..	70	70	65	64
Average time required to finish .....days..	75	75	84	83
Average daily gain.....pounds..	1.71±.022	1.79±.025	1.60±.017	1.69±.026
Feed consumed per 100 pounds of gain....do....	399	405	409	402

TABLE 8.—*Initial weights, daily gain, and 6-month weights of purebred and crossbred pigs*

[Average of purebreds paired with average of crossbreds in same litter (20 pairs)]

Item	Purebred	Crossbred	*Z*	Probability
	Pounds	*Pounds*		
Initial weight	65.3	68.4	0.22	4.4:1
Average daily gain	1.59	1.65	.22	4.4:1
Last weight	179.1	185.6	.22	4.4:1

Because all pigs of a litter did not finish the feeding test at the same time (they were removed when the individual reached a weight of 200 pounds) their final weights were not taken at a uniform age. In order to compare the average weight of all purebred pigs of a litter with that of all crossbred pigs of the same litter at the same age, it was necessary to select weights which were taken at the same time, but before any of the pigs had been removed from the experiment. The average of the 20-litter averages for purebred pigs was 179.1 pounds and for the crossbreds 185.6. Again the difference is not significant. A summary of these results is given in table 8.

In all comparisons of purebred and crossbred animals in this experiment, including weight at birth, mortality before vaccination, initial weight, rate of gain, feed consumption per 100 pounds gain, and weight at approximately 6 months of age, the only one significantly in favor of the crossbreds is birth weight. The others are in favor of the crossbreds but the difference is in no case significant. One might inquire into the probability of all or several measurements being in favor of the crossbreds when no one is significant. The question, however, is not one of simple probability because of the correlations existing among such things as rate of gain, economy of gain, and initial weights.

The literature on cross-breeding swine is by no means consistent in ascribing beneficial results to cross-breeding. As long as such a condition exists it would seem that a problem of major importance is to learn more concerning the nature of heterosis or hybrid vigor in order that predictability of cross-breeding results might be attained. The system of double mating provides a refinement in experimental technique which this problem in its present state greatly needs.

SUMMARY

Double matings were used with Duroc Jersey and Poland China swine to produce litters that contained both purebred and crossbred pigs.

A significantly larger number of pigs were produced in litters sired by two boars (mixed litters) than in litters sired by a single boar (purebred or crossbred litters).

The birth weights of purebred and crossbred pigs were subjected to three methods of analysis to determine whether the differences between them were significant. By the method considered best adapted to the problem, a small but significant difference in favor of the crossbreds was demonstrated.

Among pigs farrowed alive the strength gradings were slightly in favor of the crossbreds, but a slightly larger percentage of crossbred pigs were farrowed dead.

Mortality before vaccination was slightly less in crossbreds than in purebreds.

Small differences in favor of crossbreds were found in respect to weight at beginning of feeding test, daily rate of gain, feed per 100 pounds of gain, and weight near market age, but these differences were not statistically significant.

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